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A STUDENT'S TEXT-BOOK OF ZOOLOGY

CORRIGENDA

- Page 27. Line 10-11 of paragraph 2, for "*Rhodooma*" read "*Rhodosoma*."
- „ 167. Legend of Fig. 117, for "*Parkinson*" read "*Parkinsoni*."
- „ 177. Legend of Fig. 128, for "hedatic" read "hepatic."
- „ 183. Line 10 from bottom, for "*Gymnasteria*" read "*Gymnasterias*."
- „ 189. Fam. 1 delete the following genera *Gnathaster* Slad., *Mimaster* Slad., *Leptogonaster* Slad.
- „ 189. Line 8 of Fam. 1, for "*tenuispiins*" read "*tenuispinis*."
- „ 266. Line 10 from bottom, delete "*Pseudostichopus* Théel."
- „ 269. Line 4 from bottom, for "*Myriotrocha*" read "*Myriotrochus*."
- „ 487. Line 10 from bottom, for "*Armadillium*" read "*Armadillidium*."
- „ 540. Last line, for "*Coenobita*" read "*Cenobita*," or alter the other mentions of the genus to *Coenobita*.
- „ 573. Line 6 from bottom, for "*Opisthoptaus*" read "*Opisthopatus*."
- „ 716. From 25 line 12, 13. *Taleporia* and *Solenobia* are now classified with the *Tineidae*, which see.

A STUDENT'S TEXT-BOOK OF ZOOLOGY.

3-

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VOL. III

THE INTRODUCTION TO ARTHROPODA, THE
CRUSTACEA, AND XIPHOSURA

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LONDON

SWAN SONNENSCHN AND CO. LTD

NEW YORK: THE MACMILLAN CO.

1909

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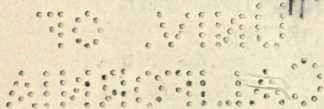
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PREFACE

IN parting with the present volume I have the satisfaction of feeling that I have accomplished the first part of the task which I set myself fourteen years ago. When I began I looked forward to executing the whole work, both Special and General Parts, myself in seven or eight years. That expectation has not been realized. Indeed had it not been for the assistance given me by my colleagues, Mr. J. J. Lister and Mr. A. E. Shipley, the present volume would have been far from completion. Thanks to their generous co-operation it is now finished, and I am in a position to turn my attention to the General Part. It is satisfactory to have finished it, but it is impossible to avoid a feeling of regret that owing to circumstances which were unforeseen when the work was commenced it has occupied so many years and that the General Part, to write which the Special Part was undertaken, is not yet begun.

The distribution of the work of this volume has been as follows: The chapters on Tunicata, Enteropneusta, Echinodermata, Onychophora and Myriapoda are by myself; the chapters on the Arthropoda in General and on the Crustacea, and the section on the Xiphosura are by Mr. Lister; and those on the Insecta and the Arachnida by Mr. Shipley.

Our thanks are especially due to Professor Herdman, Mr. Punnett, Dr. Bather, Professor MacBride, Mr. Sinclair, Dr. Calman, Mr. L. A. Borradaile, Mr. David Sharp, Mr. Hugh Scott, Professor Imms, Mr. C. Warburton and Mr. C. C. Dobell for reading the proofs and for the advice and assistance which they have given in different parts of the volume.

Our thanks are further due to those authors and publishers who have allowed us to use illustrations which have

appeared in other works. The sources of these are acknowledged, but we must especially mention Claus's *Lehrbuch*, Shipley & MacBride's *Zoology*, Bronn's *Thierreich*, Korschelt & Heider's *Textbook of Embryology*, Delage & Hérourard's *Zoologie Concrète*, Perrier's *Traité de Zoologie*, the *Cambridge Natural History*, Lang's *Textbook of Comparative Anatomy*, Zittel's *Grundzüge der Palaeontologie*, Lankester's *Treatise on Zoology*.

I have also to state that the drawings from which figures 105 and 132 were engraved were made by Mr. J. C. Simpson under the direction of Professor MacBride.

Now that the work is completed something must be said as to its architectural plan. This has been criticized (see, for example, the review in *Nature*, November 23, 1905) on the ground that the Arthropods are separated from the Annelids, and that the Tunicates and Enteropneusta are placed at the end of the Chordata. In the first volume the clue given by the coelom is mainly followed and this leads from the Annelids to the enterocoelic phyla the Phoronidea, the Brachiopoda and the Chaetognatha. Having reached this point it was not possible to treat the Arthropoda until after the Enterocoela were finished. This accounts for the position of the Arthropoda at the end of the work. It may be objected that the Arthropoda should have come after the Annelida in volume I. But this would have involved the inconvenience of separating the Gephyrea Achaeta from the Gephyrea Armata, and the Brachiopoda and Polyzoa from the Chaetopoda. Moreover, the Arthropoda differ so fundamentally from the Annelida in their coelomic arrangements and are such an enormous and self-contained group that it did not appear that any practical disadvantage would follow upon their separation from the latter which in some features of their organization they so closely follow. In fact we are here confronted with a difficulty which the systematic Zoologist meets at every turn and to which attention has often been called in the course of the work. When there is more than one clue, as there nearly always is, which shall we follow? We are obliged to adopt a linear arrangement, whereas Nature

is content with nothing less than arrangement in three dimensions.

Following then the clue of the coelom and having reached so near the Chordata, it seemed natural and proper to take them after the Chaetognatha. I might of course have placed the Echinoderms here and treated the Enteropneusta after them. That was in fact the original intention, but after careful consideration there seemed no reason based on zoological affinity why this should be done and it would have been almost an outrage to have placed the Echinoderms next to Sagitta. It was accordingly decided to take the Chordata at this point, beginning with Amphioxus and reserving the Enteropneusta to the end to lead on to the Echinoderms.

Though I offer this explanation I quite recognize the validity of the criticism. All zoological arrangements are compromises, and none of them can be, now or ever, entirely natural.

A. SEDGWICK.

CAMBRIDGE,

November 25, 1908.

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A. SEDGWICK.

CAMBRIDGE,

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CHAPTER I.

PHYLUM TUNICATA* (UROCHORDA).

Fixed or pelagic, solitary or colonial animals enclosed in a tunic or test, which is largely composed of a substance allied to cellulose. They have an atrial cavity and a large pharynx with perforated walls. The larva is tadpole-shaped and possesses a hollow dorsal central nervous system, and a notochord in the caudal region.

* Savigny, *Mémoires sur les animaux sans vertèbres*, 2, Paris, 1816. Milne-Edwards, *Obs. sur les Ascidies composées des côtes de la Manche*, *Mém. Ac. Sc. Paris*, 18, 1842. Huxley, *On the anatomy and physiology of Salpa and Pyrosoma*, *Phil. Trans.* 1851. *Id. Anat. and devel. of Pyrosoma*, *Trans. Lin. Soc.* 23, 1860. Krohn, *Die Entwick. v. Phallusia mamillata*, *Müller's Arch.* 1852. Macdonald, *On Chondrostachys*, *Ann. and Mag. Nat. Hist.* (3), 1, p. 401, 1858, and *On Diplosoma*, *Linn. Trans.* 22, 1859. A. Hancock, *Anat. and Phys. Tunicata*, *Journ. Lin. Soc.*, 9, 1867. Kowalevsky, *Entwick. d. einfachen Ascidien*, *Mem. Acad. Sc. St. Petersburg* (7), 10, 1866, and *Arch. f. Mik. Anat.*, 7, 1871. *Id. Beiträge z. Bildung des Mantels d. Ascidien*, *Mem. Acad. Sc. St. Petersburg* (7), 38, 1892. Giard, *Rech. s. les Ascidies composées*, *Arch. Zool. Exp. Gen.* i. p. 501, 1872; *Cont. à l'histoire nat. des Synascidies*, *ibid.*, 2, p. 481. Lacaze-Duthiers, *Les Ascidies simples des côtes de France*, *Arch. Zool. Exp. Gen.* 3, 1874, p. 119, and 6, 1877, p. 457. L.-Duthiers et Delage, *Ét. anat. et zool. sur les Cynthidies*, *Arch. Zool. Exp. Gen.* 7, 1889, p. 519. *Id.*, *Études sur les Ascidies des côtes de France (Cynthiidae)*, *Mém. Acad. Inst. France*. Roule, *Rech. s. les Ascidies simple des côtes de Provence*, *Ann. du Mus. Hist. Nat. Marseille*, 2, 1884, and *Ann. d. Sci. Nat.* (6), 20, 1886; *id.*, *Revision des espèces de Phallusiadées des côtes de Provence*, *Rec. Zool. Suisse*, 3, 1887. Julin, *Rech. s. l'organisme des Ascidies simples*, *Arch. Biol.* 2, 1881. v. Drasche, *Die Synascidien der Bucht von Rovigno*, Wien., 1883. Herdman, *Report upon the Tunicata collected during the voyage of H.M.S Challenger*, *Chall. Reports*, Pt. 1, *Asc. simplices*, 1882, Pt. 2, *Asc. compositae*, 1886, Pt. 3, *Salpiformes, Thaliacea and Larvacea*, 1888; *id.*, *A revised classification of the Tunicata*, *Journ. Lin. Soc.* 23, 1891. van Beneden and Julin, *Rech. s. la morphologie des Tuniciers*, *Arch. Biol.* 6 and 7, 1886. Lahille, *Recherches sur les Tuniciers des côtes de France*, Toulouse, 1890. Caullery, *Cont. à l'étude des Ascidies composées*, *Bull. Sc. France et Belg.*, 1895. Willey, *Studies on the Protochordata*, *Q.J.M.S.*, 34 and 35, 1893. *Id.*, *On the protostigmata of Molgula manhattensis*, *Q.J.M.S.*, 44, 1900, p. 141. Seeliger, *Tunicata*, in *Brcnn's Thierreich*, 1893 and onwards. Delage et Hérouard, *Traité des Zoologie Concrète*, 8, Paris, 1898. Korschelt and Heider, *Text-Book of Embryology*, English Translation, Pt. 4, London, 1900. Selys Lonchamps et Damas, *Le dével-post-embryonnaire et l'anatomie de Molgula*, *Arch. Biol.* 17, 1904, p. 385. Damas, *Contribution à l'étude des Tuniciers*, *Arch. Biologie*, 20, 1904, p. 745.

The *Tunicata* are entirely marine animals. They comprise sessile forms, attached to foreign bodies in the sea, and pelagic forms which float freely, principally in the surface waters of the ocean. Many of them live in colonies and most possess the power of asexual increase by budding.

Their place in the system was for a long time unsettled. By Linnaeus they were placed partly amongst the *Mollusca* and partly amongst the *Zoophyta*, and this example was followed until the beginning of the last century, when as a result of the anatomical investigations of Cuvier, Lamarck and Savigny, the true nature of the compound Ascidians and their relationship to the simple Ascidians were recognized. As a result, the group *Tunicata* was established by Lamarck in the year 1816,* and placed between his *Radiata* and *Vermes*. Lamarck recognized their distinctness from the *Mollusca*, but Cuvier (*Règne Animal*, 1817) failed to do this and placed them with the *Acephala*. The views of Cuvier predominated and the *Tunicata* were regarded as Molluscs until the middle of last century. At about that time suspicions arose as to the correctness of Cuvier's view, and the class *Molluscoidea* was in 1844 suggested by H. Milne-Edwards to comprise the *Polyzoa*, *Brachiopoda* and *Tunicata*. At this point the discussion remained, until the publication in 1866 of Kowalevsky's work on the development of the simple Ascidians. He there showed that the tailed larva, first observed by Milne-Edwards and afterwards described by Krohn, is evolved by a process closely resembling the early development of the vertebrate embryo, that it possesses a dorsal tubular nervous system and a notochord, and that the branchial basketwork of the adult is derived from simple stigmatic apertures which can be fairly brought into relation with the gill-slits of the Vertebrata. Various far-reaching phylogenetic hypotheses have been based upon this discovery, amongst the most astonishing of which must surely be ranked that which assigns to the *Tunicata* a place in the direct line of vertebrate ancestry. But putting all these on one side, as indeed we may safely do without any appreciable loss to zoology, there still remains this important result from Kowalevsky's famous investigation; it has settled finally the systematic position of the *Tunicata*. Henceforth they must be placed, if not actually within, still in close association

* *Histoire naturelle des animaux sans vertèbres*, 3, 1816.

with the vertebrate phylum, and to Kowalevsky must be assigned the first place amongst the many distinguished workers whose labours have built up our knowledge of tunicate morphology. But the *Tunicata* have other claims to the special attention of zoologists. Most of them possess the power of asexual reproduction by budding. Not only is this noteworthy in a group so near the Vertebrata, but the phenomenon is remarkable for the variable manner in which it is effected. The condition of the coelom appears to be highly peculiar, and the presence outside the ectoderm of a layer containing blood-vessels and nucleated elements is a feature unique in the animal kingdom.

As a type of the *Tunicata* we shall take a common example of the simple Ascidians, *Ciona intestinalis*. *Ciona* has an elongated form (Fig. 1). At one end, which we shall call the posterior, it is attached by processes of the test to the substratum; at the other end, which we shall call the anterior, is the mouth-opening, or, as it is often called, the inhalent siphon. A little distance from the mouth on one side of the body is a second opening, the aperture of the atrial cavity or exhalent opening (Fig. 1, 2). The side on which this is placed is called dorsal. The side opposite to that on which the atrial opening is placed is the ventral surface. The whole body is covered by a semi-transparent gelatinous coat, called the **tunic** or **test**. The test is a thick, hyaline,

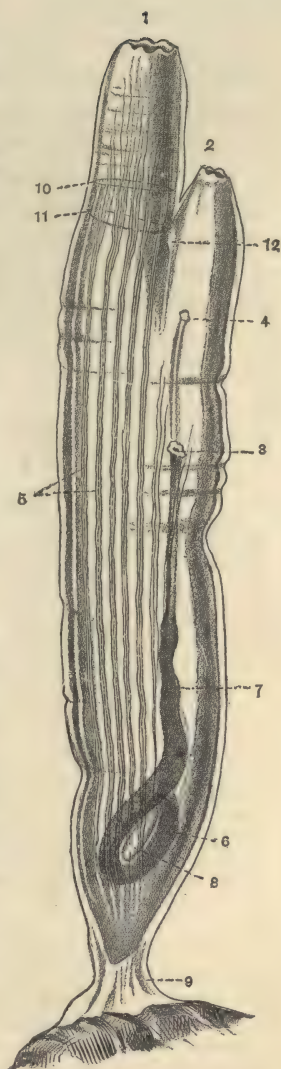


FIG. 1.—*Ciona intestinalis*, life size (after Shipley and MacBride). Some of the organs can be seen through the semi-transparent test. 1 mouth; 2 atrial aperture; 3 anus; 4 genital opening; 5 muscles of body wall; 6 stomach; 7 rectum; 8 ovary; 9 stolon of attachment; 10 tentacular ring; 11 peripharyngeal ring; 12 nerve-ganglion.

cuticular layer containing cellulose. It is lined internally by a layer of ectoderm cells which in the first instance secretes it. The remainder of the body wall, consisting of unstriped muscle and connective tissue and in the region of the atrial cavity of lining atrial epithelium, constitutes the **mantle**. In the living animal it is in contact with the ectoderm, but in spirit specimens it frequently shrinks away leaving a space between the two, the only points of contact being the mouth and atrial apertures, and the point near the hind end of the endostyle, where the blood-vessels pass across from the mantle to the test.

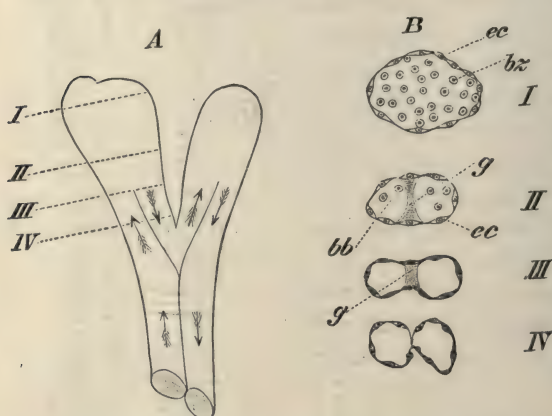


FIG. 2.—Vessel from the test of *Phallusia mammillata* $\times 250$ (after Seeliger from Bronn). A end of test-vessel in surface view. B series of four sections (I-IV) through a terminal test-vessel made at the lines marked I-IV in A. The arrows indicate the direction of the blood-stream. bb cavity of blood-vessel; bz blood corpuscles; ec ectodermal wall of the vessel; g gelatinous septum, which continues the separation between the two blood-streams for a short distance (II and III) into the terminal bulb.

The test is a cuticular secretion of the ectoderm, of very various consistency and colour in the different forms. When it is first formed it is structureless, but it frequently becomes fibrillated and in most Tunicates processes of the body wall containing blood-vessels and nucleated protoplasmic elements soon make their way into it. The vascular processes may arise at

one or more points. They branch in the test and eventually end in terminal swellings. Each blood-vessel is double, except in the terminal bulb, where the two are in communication (Fig. 2, A). The nucleated protoplasmic elements of the test are for the most part mesodermal in origin, having passed through the ectoderm. Some of them have a peculiar vesicular form, having developed large vacuoles (vesicular cells). Others contain pigment, while yet others may secrete calcareous (Synascidians) or siliceous (Salps) spicules.

The mantle contains a considerable development of muscular fibres, which confer upon it a great power of contractility. At the apertures the muscles are arranged as sphincters.

The mouth is surrounded by eight small lobe-like projections of the mantle, between which red pigment spots are placed. It leads

into a short tube—the buccal cavity or stomodaeum—into which the test is prolonged as a lining. This passes into a large cavity, the **pharynx** or branchial sac (Fig. 3), the anterior end of which is marked by a row of small hollow tentacles containing blood (2). A little further back the pharynx is encircled by a grooved ridge called the *peripharyngeal band* (3). The portion of the ridge between the tentacular row and the peripharyngeal band is called the *prebranchial zone*: it is devoid of gill apertures, but bears just anterior to the peripharyngeal band in the dorsal middle line a funnel-shaped ciliated pit, called the **dorsal tubercle** or ciliated funnel (Fig. 3, 13, Fig. 4, *i'*). Into this pit, which is lined by ciliated columnar cells, there opens in all Tunica, except the Salpidae (see below, p. 47) and the phorozoid of *Doliolum*

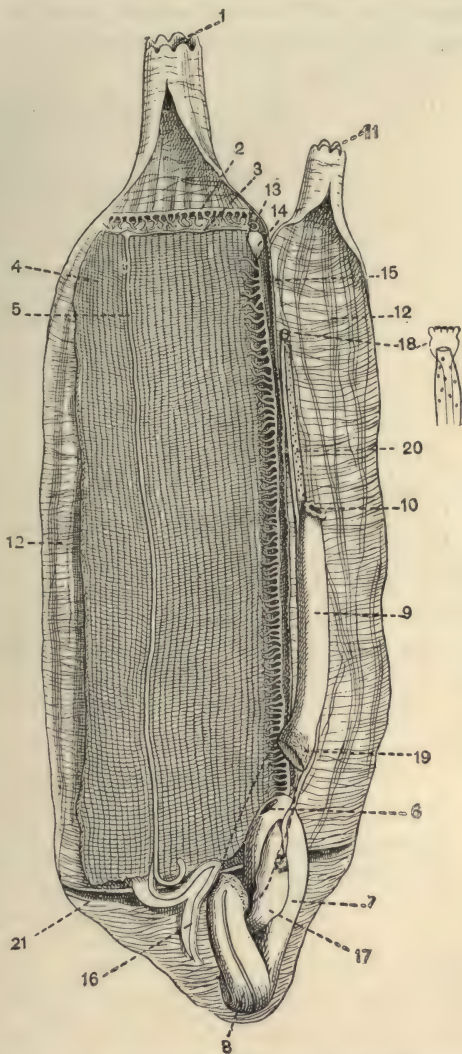


FIG. 3.—Side view of *Ciona intestinalis*. The pharynx and atrial cavity have been opened on the left side (after Shipley and MacBride). 1 mouth; 2 tentacles; 3 peripharyngeal band; 4 wall of pharynx; 5 endostyle; 6 opening from pharynx into oesophagus; 7 stomach; 8 intestine showing typhlosole; 9 rectum; 10 anus; 11 atrial aperture; 12 inner surface of body wall (mantle) showing muscles; 13 dorsal tubercle; 14 subneural gland and ganglion; 15 cut edge of pharynx wall; 16 heart in pericardium; 17 ovary; 18 pore of vas deferens; 19 testicular tubes on intestine; 20 oviduct; 21 anterior boundary of body-cavity (epicardial cavity).

affine, the duct of the neural gland. The walls of the pit are innervated by nerve fibres from the ganglion, and some of its lining cells appear to be sensory. The **subneural gland**, the

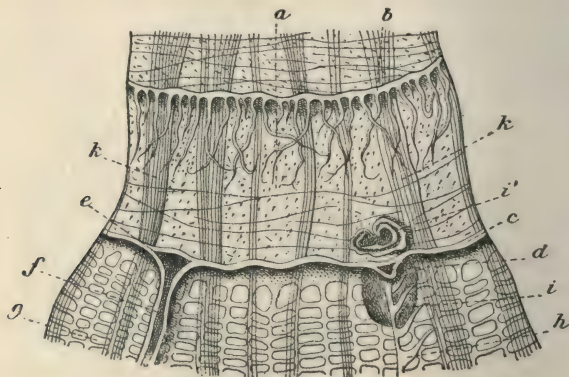


FIG. 4.—Inner surface of buccal cavity and of the anterior part of the pharynx of *Ciona*. *a* prebranchial zone; *b* tentacular circlet; *c* peripharyngeal band; *d* epibranchial groove; *e* union of endostyle with peripharyngeal band; *f* endostyle; *g* pharyngeal apertures; *h* dorsal lamina with languets; *i* subneural gland; *i'* dorsal tubercle; *k* longitudinal muscle (after Vogt and Yung).

duct of which is lined by cubical non-ciliated cells, is in close contact with the ganglion, generally on its ventral side, but it sometimes lies dorsal to the ganglion (*Cynthia*, *Molgula*, *Botryllus*, etc.).

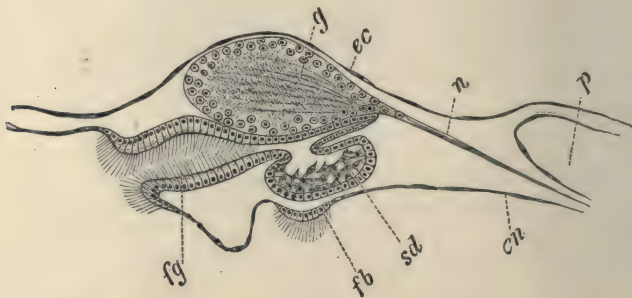


FIG. 5.—Diagrammatic longitudinal section through the ganglion and subneural gland of *Clavelina* (after Seeliger from Bronn). *ec* ectoderm; *en* endoderm; *fb* peripharyngeal band (not grooved in this form); *fg* ciliated pit (dorsal tubercle); *g* ganglion; *n* nerve; *p* atrial cavity; *sd* subneural gland.

The prebranchial zone is in some forms covered with small papilliform projections. The opening of the ciliated funnel varies much in form. In a few cases it is circular. More often it is semicircular or horseshoe shaped (Fig. 4). Sometimes the horns of the semicircle are spirally curved

and occasionally the lips fuse in places so that the opening becomes subdivided into many (*Ascidia marioni* and *atra*, *Phallusia mammillata*). The neural gland is said to be derived from a portion of the cranial vesicle of the larva, which as is well known acquires a secondary opening into the anterior end of the alimentary canal. It is clearly glandular, but its exact function is quite unknown. It has been supposed, without sufficient reason, to be a renal organ. Its secretion is formed by the disintegration of cells proliferated from its epithelium.

The **peripharyngeal band** consists in *Ciona* of two ridges placed close together and encircling the pharynx at the hind end of the

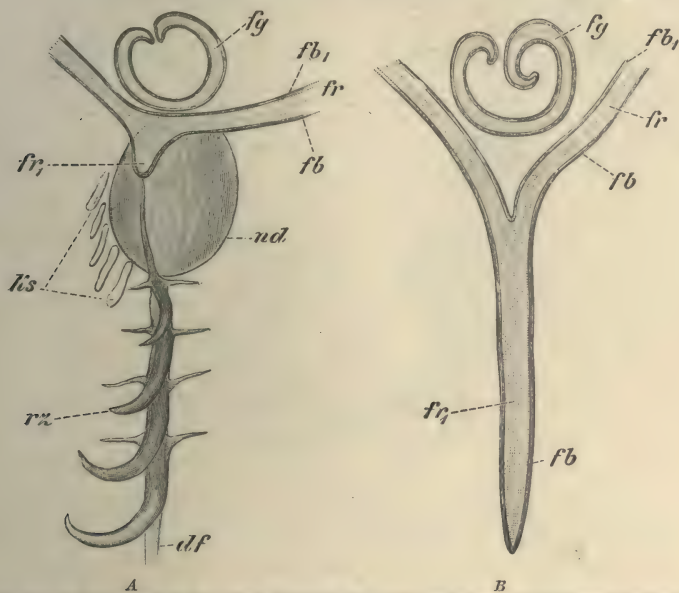


FIG. 6.—A The region of the dorsal tubercle and of the anterior end of the dorsal lamina of a young *Ciona intestinalis*, from within. B Dorsal tubercle and peripharyngeal band of *Ascidia*, diagrammatic (after Seeliger). *df* dorsal lamina; *fb*, *fb* anterior and posterior ridges of peripharyngeal band; *fg* dorsal tubercle; *fr* groove of the peripharyngeal band; *fr*, epibranchial groove; *ks* gill-slits; *nd* neural gland; *rz* languet of dorsal lamina.

prebranchial zone (Fig. 4, c). Of these the anterior is without cilia (Fig. 6 A, *fb*₁), while the posterior has cilia on its front side. They enclose between them a groove which may be called the *peribranchial groove*. The anterior and smaller ridge forms a complete circle, whereas the posterior ridge is incomplete ventrally, each side of it being continuous with the marginal ciliated tract of the endostyle (Fig. 4, e). Dorsally the posterior ridge is deflected backwards and joins its fellow (Fig. 6). The space enclosed by this backwardly deflected part of the posterior ridge

is an enlarged portion of the peribranchial groove and is called the *epibranchial groove* (Fig. 6, *fr*₁). There is a considerable interval, covered by a flat epithelium only, between it and the first languet of the dorsal lamina (Fig 6 *A*). In some forms the deflected part of the posterior ridge is of considerable length (Fig. 6 *B*), reaching to the anterior end of the dorsal lamina, on to which it is continuous. In such cases the epibranchial groove may be very deep. It is lined by a ciliated epithelium similar to that of the peripharyngeal groove of which it is an extension.

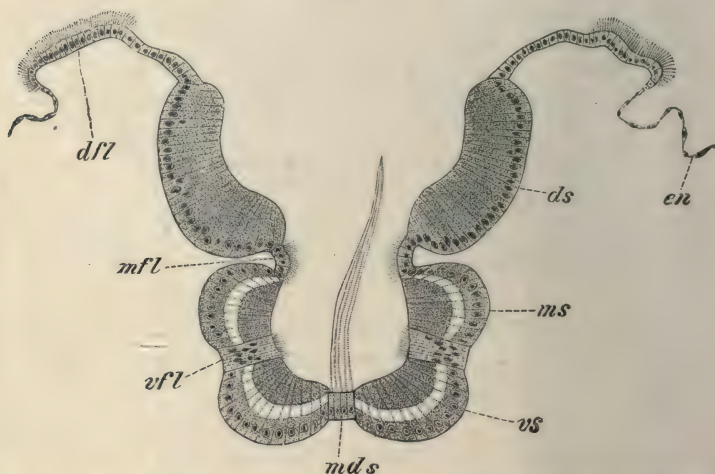


FIG. 7.—Transverse section through the endostyle of *Clavelina lepadiformis*, semidiagrammatic (after Seeliger). *ds* dorsal; *ms* median and *vs* ventral glandular band; *dfl* dorsal (marginal); *mfl* median; *vfl* ventral ciliated band; *en* endoderm of lateral wall of pharynx; *mds* median strip of flagellated cells.

In some forms the anterior as well as the posterior face of the peripharyngeal furrow is ciliated. In *Appendicularia* and some synascidians (e.g. *Botryllus*) the peripharyngeal band consists of a single ciliated ridge only.

The **endostyle** is a groove lined partly by glandular and partly by ciliated cells extending the whole length of the median ventral wall of the pharynx (Fig. 3). It presents but little variation of structure. Typically it consists on each side of three bands of large glandular cells, and of three bands of smaller ciliated cells (Fig. 7). In the ventral middle line there is a narrow band of small cells carrying long flagella. Anteriorly and posteriorly the endostyle, excluding the marginal ciliated bands, is continued into small blind pockets of the pharynx (Fig. 3), of

which that at the posterior end is the largest. The marginal ciliated bands are continuous in front with the peripharyngeal band (posterior ridge, if both are present) and behind with the ciliated ridge or groove (*retropharyngeal band*) which passes from the hind end of the endostyle along the median line of the posterior wall of the pharynx to the opening of the oesophagus.

The retropharyngeal band may be a single ciliated ridge continued back from one of the lips of the endostyle (most synascidians), or a single ridge formed by the fusion of both margins (*Molgulidae*), or finally, as in *Ciona*, both lips may be continued back with a groove between them.

The **dorsal lamina** is, in most monascidians and many synascidians, a fold of the dorsal pharyngeal wall containing blood sinuses and extending from the anterior end of the pharynx to the opening of the oesophagus. It may be continuous with or separated from the peripharyngeal ridge (see above). The cells covering it are somewhat more columnar than those over the lateral walls of the pharynx and are for the most part ciliated. In a few monascidians (e.g. *Ciona*) and some synascidians it has the form of a series of isolated variously-shaped processes of the dorsal wall, called **languets** (Fig. 3). These two forms of it are connected by a condition in which it consists of a continuous membrane carrying processes at intervals. The languets and the processes last mentioned occur at the dorsal ends of the transverse bars of the pharynx. The dorsal lamina, whether consisting of languets or of a lamella, is curved, generally to the right, so as to bound a groove leading to the oesophageal aperture. The posterior termination of the dorsal lamina varies considerably and is often difficult to determine. It usually seems to pass round the left side of the oesophageal opening and become continuous with the retropharyngeal band, or it gradually dies away.

The lateral walls of the pharynx have the form of a basketwork and are pierced by numerous, usually longitudinally elongated apertures, placed in transverse rows. These are the *gill-slits* or *stigmata*. They are usually distributed all over the lateral pharyngeal wall behind the peripharyngeal band, but are sometimes absent from its posterior part (Fig. 8).

The number of transverse rows of stigmata and the number of stigmata in a row are very variable, not only in different species but also in individuals of the same species. It would

appear that the number, both of rows and of stigmata in a row, increases with the growth of the animal. Speaking

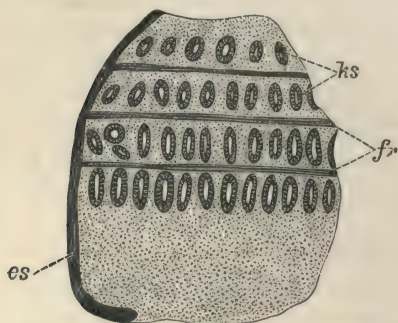


FIG. 8.—Branchial basket of *Leptoclinum Edwardsi* from the left (from Seeliger after Herdman). *es* endostyle; *fr* transverse bars; *ks* gill slits (stigmata).

generally, the number is smallest in the synascidians and largest in the monascidians. After full size has been attained and development completed, there is never less than three rows (species of *Didemnum*, *Distoma*, etc.), but in large specimens of *Ciona intestinalis* there may be 250 rows, and in *Phallusia mammillata* as many as 500. The number

of stigmata in a row may be as small as three (*Distoma deeratum*) and as many as 500 in large specimens of *Phallusia*.

The exact method of formation of new stigmata* is disputed. It appears probable that in the larva a certain number of primary stigmata are formed as perforations of the pharyngeal wall (three on each side in *Ciona* according to Willey), and that it is by the division of these and not by the formation of new perforations that new stigmata are developed.

The stigmata open externally into the atrial cavity which surrounds the pharynx except in the ventral middle line, and the epithelium lining them is ciliated. The walls of the pharynx between the transverse rows of stigmata may be called transverse bars, and those between the stigmata of a row the longitudinal bars. Both transverse and longitudinal bars contain blood sinuses,—the transverse and longitudinal vessels respectively. In many ascidians vascular papillae project from the transverse bars into the cavity of the pharynx. These may bifurcate at their ends and, extending up and down the pharyngeal wall, join similar branches of

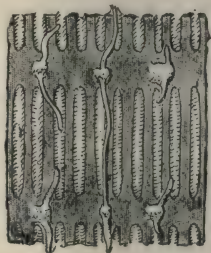
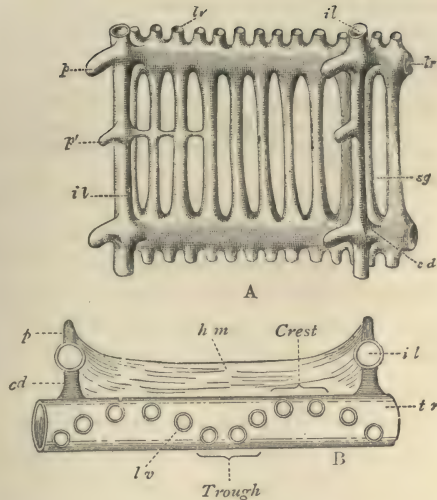


FIG. 8.—Portion of the wall of the pharynx of *Perophora banyulensis*, showing the bifurcated papillae of the transverse bars, partly joining to form an internal longitudinal bar (from Delage and Hérouard).

* Willey, *op. cit.*, *Q.J.M.S.*, 44, 1900, p. 173. Julin, *Z. f. w. Z.*, 76, 1904 p. 544. Damas, *op. cit.*, 1904.

neighbouring papillae (Fig. 8). In this way internal longitudinal bars, connected to the transverse bars and extending the whole length of the pharynx, are often formed (Fig. 9 A). At the points where the internal longitudinal bars are connected to the transverse bars, small papillae are often found projecting into the pharynx, and horizontal membranes are often present along the transverse bars, connecting these papillae (Figs. 10 and 11).



FIGS. 9 and 10.—A Part of pharynx of *Ascidia* from inside. B Transverse section of the same. *tr* transverse bar; *cd* connection of internal longitudinal bar to transverse bar; *hm* horizontal membrane; *il* internal longitudinal bar; *lv* fine longitudinal bars; *tr* transverse bar; *p*, *p'* papillae; *sg* stigma (from Herdman).

The stigmata vary much in form. They may be circular, oval, slit-like, or spirally coiled. Their long axis is generally parallel to the long axis of the animal. In a few, e.g. *Boltenia elegans*, *Cynthia villosa*, it is transverse. In a few deep-sea forms (*Culeolus*, *Fungulus*, *Bathyoncus*, *Pharyngodictyon*) the stigmata are large and square and there are no longi-

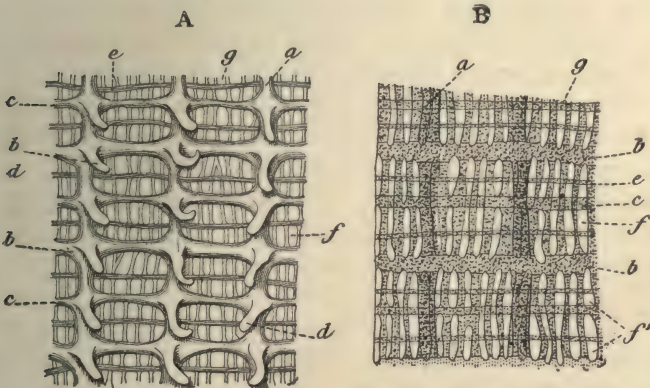


FIG. 11.—Structure of pharyngeal wall of *Ciona intestinalis* (from Vogt and Yung). A from within. B from outside. *a* internal longitudinal bar; *b* transverse bar of the first order; *c*, *g* transverse bar of the second order; *d* papillae projecting into cavity of pharynx from the internal longitudinal bar; *e* transverse bar of the third order; *f*, *f'* stigmata.

tudinal bars except the internal longitudinal or what are identified as the internal longitudinal (Fig. 20). This condition has been interpreted as being due to the absorption of the fine longitudinal bars and partial confluence of the stigmata of a row. It may however be due to the simple enlargement of the stigmata, no internal longitudinal bars being present.

The side walls of the pharynx are in some forms folded longitudinally and the number of folds varies in the different types.

The function of these various organs would appear to be as follows. The glandular cells of the endostyle secrete a slimy mucous substance which is moved forwards by ciliary currents along the endostylar groove to the peripharyngeal band. Here it is reinforced by mucus secreted by the gland cells present in that organ, and kept in circular movement by ciliary action round the entrance to the pharynx. While thus moving the slime entangles within itself the minute organisms which enter the mouth in the respiratory current of water, and from time to time portions of it so charged become detached and pass down along the dorsal lamina to the oesophageal opening. The main body of water which enters the pharynx is thus deprived of its floating contents and passed out through the gill-slits into the atrial cavity and out by the atrial aperture.

It is possible that a certain amount of slime from the hind end of the endostyle passes back direct to the oesophagus along the retropharyngeal band. It has also been suggested that the neural gland secretes mucus which reinforces the endostylar mucus at the peripharyngeal band.

The **atrial cavity**, or peribranchial cavity as it is sometimes called, entirely surrounds that part of the pharynx which is perforated by gill-slits except in the middle ventral line and for a short distance at the anterior end of the dorsal lamina (Fig. 12). It opens to the exterior by the atrial aperture and communicates with the pharynx by the stigmata; the anus and genital ducts also open into it. Its lining epithelium which is ectodermal is closely applied to the pharyngeal wall and is continuous through the gill-slits with the endoderm of the pharynx. Water continually flows into it through the gill-slits and passes out by the atrial aperture. It is traversed by vascular strands which pass from the wall of the pharynx to the outer (mantle) wall, and it is developed as two dorso-lateral invaginations of ectoderm which unite dorsally and extend laterally round the pharynx as far as the endostyle. The dorsal part of it is frequently called the cloaca. It is into this part that the anus and genital ducts open.

In most *Tunicata* the digestive organs are placed behind the pharynx and atrial cavity (Fig. 3), and the part of the body containing them is frequently called the abdomen, as opposed to the thorax or pharyngeal region. In monascidians, however, the pharynx extends the whole length of the body and the digestive

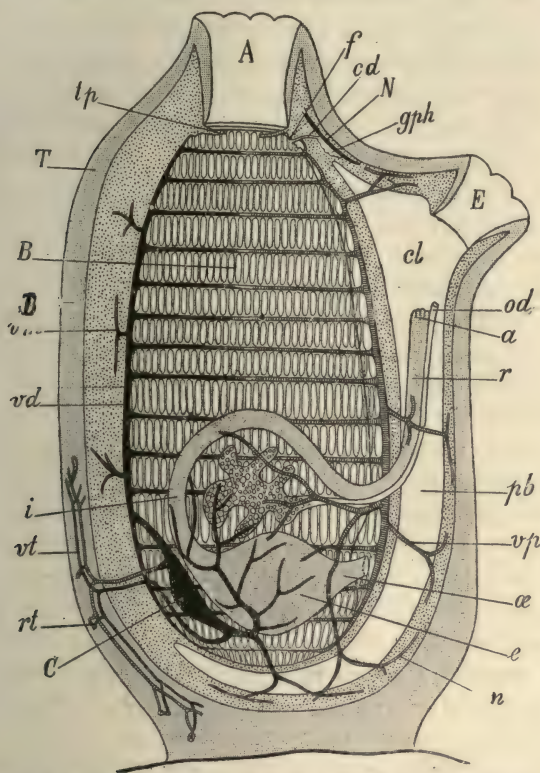


FIG. 12.—Diagram showing the anatomy of *Ascidia* (after Herdman, from Perrier). *A* mouth; *a* anus; *B* pharynx; *C* heart; *cd* duct of hyponeural gland; *cl* atrial cavity; *E* exhalant aperture; *est* stomach; *f* dorsal tubercle (ciliated pit); *gph* subneural gland; *i* intestine; *m* mantle; *N* ganglion; *od* genital duct; *oe* oesophagus; *pb* atrial cavity; *rt* terminal ampullae of the test-vessels; *T* tunic or test; *tp* tentacles; *vd* endostylar vessel; *vm* blood-vessels of mantle; *vp* vascular strands crossing the atrial cavity; *vt* blood-vessels of the test; *r* rectum.

viscera are placed on one side of it, usually the left (Fig. 12). They are embedded in the mantle and usually cause a projection into the atrial cavity. *Ciona* forms an exception to this rule.

The digestive canal consists of oesophagus, stomach, intestine and rectum. It is twisted upon itself in various ways and ends by opening into the atrial cavity in the middle line either at

its hind end or anteriorly. In the latter case the rectum is of considerable extent and lies along the dorsal wall of the pharynx adjacent to the dorsal lamina (Figs. 3 and 12).

The oesophagus leaves the pharynx dorsally, usually postero-dorsally, in the middle line at or near the end of the dorsal lamina. It passes into the dilated stomach, the other end of which is continued as the intestine which finally passes into the rectum. There is very generally present a gland which consists of fine colourless tubules ramifying over the stomach and intestine and opening into the pyloric end of the stomach or first part of the intestine; it is called the *pyloric gland* (hyaline organ). In a few forms (*Molgulidae*, many *Cynthiidae*, etc.) glandular masses which have been compared to a liver, are found on the walls of the stomach. A longitudinal fold (typhlosole) of the intestinal wall, projecting into the lumen of the intestine, is often present. The epithelium of the digestive tube is partly ciliated and partly glandular.

The **central nervous system** consists of an elongated ganglion embedded in the mantle on the dorsal surface of the body between the mouth and atrial aperture (Fig. 3, 14, Fig. 5, g). It gives off nerves from its front and hind ends. A median posterior nerve containing nerve cells is present in many forms: it is called the visceral nerve and is supposed to be the posterior part of the nerve cord of the larva. The ganglion is solid and consists of nerve fibres in the centre and nerve cells at the periphery.

Sense organs. Organs of general sensation in the form of tactile hairs are always present. But except in Thaliacea and Appendiculariae, and possibly *Pyrosoma*, visual and auditory organs are not found. The red pigment spots placed between the lobes of the mouth and of the atrial aperture may however have some visual function.

The salps and *Pyrosoma* possess **phosphorescent** organs.

The **coelom** of the *Tunicata* is not thoroughly understood. The general spaces and sinuses of the body are not coelomic but vascular (haemocoelic). They are frequently spoken of as constituting the primary body-cavity and as being a persistent part of the segmentation cavity of the early embryo. In our opinion however this nomenclature is misleading and as a matter of fact the reputed embryonic derivation on which the terminology

is based does not occur. The vascular space in Tunicates as in other forms is a space in the so-called mesodermal tissues of the body. As it frequently appears before the mesoderm is extensively developed, it seems to lie between ectoderm and endoderm and to be bounded by these layers, and in this respect has the relations of the segmentation cavity or blastocoel. But it is not derived from the blastocoel, which closes up by the coming together of the ectoderm and endoderm on the completion of the gastrula invagination.

Excluding the generative organs, which will be dealt with below, it would appear that the only possible representatives of the coelom are the pericardium and the epicardium. The pericardium is a closed epithelial sac found in all or almost all Tunicates in the neighbourhood of the stomach and not far from the hind end of the endostyle. It is developed in the embryo, in some forms at any rate, as a diverticulum of the epicardium (see below). One side of it, generally the dorsal, is invaginated upon the rest much as a blastosphere is invaginated to form a gastrula. The space enclosed by the invaginated wall and corresponding to the cavity of the gastrula is the *heart*. As the aperture of invagination never completely closes, the cavity of the heart communicates, generally at its two ends, with the haemocoelic spaces of the body. The contraction of the heart is effected by the invaginated wall which acquires cross-striated contractile fibres on that side of it turned towards its cavity; the inner side, i.e. the side turned towards the pericardial cavity remaining epithelial. It results from this mode of origin that the heart is without an endothelial lining.

The **epicardium** is usually found only in the budding forms. It opens into the pharynx by a median opening just behind the endostyle, or by two openings, one on each side of the middle line between the end of the endostyle and the oesophagus. It passes backwards and extends into the abdomen (*Clavelinidae*, *Polyclinidae*, *Distomidae*), where it is closely applied to the dorsal wall of the pericardium, forming indeed, when this is invaginated, the actual dorsal wall of the heart. In these forms it has been shown that the pericardium is actually developed from it, and it always extends into the stolon and gives rise to an important constituent of the buds. In *Pyrosoma* and the *Thaliacea* it has not this close connexion with the pericardium

but extends as a single tube into the budding stolon. The identification of this pharyngeal diverticulum with the coelom rests upon the assumption that the pericardium is coelomic, and upon its structure and developmental relations to the pericardium and pharynx in the *Clavelinidae*, *Polyclinidae*, and *Distomidae*. In *Ciona* an epicardium is present. It has the form of a perivisceral cavity in relation with the digestive viscera and communicates with the pharynx by two openings placed one on each side of the retropharyngeal groove * (p. 9). It is indeed a completely double structure and develops as such from the hind end of the pharynx. It appears that in *Ciona* the pericardium does not develop from this cavity † as it does in *Clavelinidae* and some other synascidians. So far as is known *Ciona* is the only Tunicate with anything corresponding to the coelomic body-cavity of other groups, and it is apparently the only monascidian in which the epicardium is developed. It is possible however that with the extension of our knowledge both these tentative statements may be shown to be erroneous.

Vascular System. There appears to be a certain number of main blood channels, but the greater part of the circulation takes place in irregular sinus-like spaces in the mesoderm which are said to be without definite walls. The heart is a simple sac or tube formed as above described by infolding of the wall of one side of the pericardium. In *Appendiculariae* (see p. 64) there is hardly any infolding, and the heart is little more than a contractile membrane. In other forms the infolding is considerable, and the opening of invagination is closed, except at the two ends where it remains open, either by union of its lips or by the closely apposed epicardium. The heart, like the vascular channels of the body, appears to be without endothelial lining, and its walls contain cross-striped muscular fibres. It varies considerably in position; it is generally placed near the stomach not far from the hind end of the endostyle. In the *Polyclinidae* it is in the postabdomen. In *Ciona* it is V-shaped and lies in the intestinal loop somewhat to the right of the stomach (Fig. 3).

Each end of the heart is continuous with a blood-channel. The one of these extends on the ventral side of the pharynx

* Newstead, *Q.J.M.S.* 35, 1893, p. 119.

† De Selys-Longchamps, *Arch. Biol.*, 17, 1901, p. 499.

beneath the endostyle, giving off near its origin a branch to the test (Fig. 12). The other after giving off a branch to the test, which accompanies the branch from the endostylar vessel, is distributed to the digestive viscera, gonads and body wall. The endostylar vessel communicates with the sinuses in the pharyngeal wall and these again with a dorsal vessel running along the dorsal lamina. This posteriorly is distributed to the viscera and body wall, whence the blood is returned to the posterior end of the heart. It is a peculiarity very generally observable in Tunicata that the heart contracts a certain number of times in one direction and then a similar number of times in the opposite direction. Thus for a certain number of beats it acts as a respiratory heart driving the blood to the respiratory organs and thence to the system. It then reverses its action and becomes a systemic heart driving the blood first to the system and thence to the respiratory organs.*

The blood is colourless and contains nucleated corpuscles. These are generally colourless and amoeboid, but some of them generally contain pigment, either yellow, red, brown or blue.

In the *Botryllidae* the terminal branches of the test-vessels are dilated into ampulla-like sacs which have rhythmically contractile walls and assist in the circulation of the colony.

The **renal organs** † are but little understood and appear to have no relation with the coelom. The only structures to which a renal function has been ascribed are some vesicular bodies containing concretions of uric acid and other substances, and placed in the walls of the intestine, in the mantle and sometimes in other places. These structures which have not been found in all Tunicates are without a duct; so that the excretory matters cannot escape. In the *Molgulidae* there is a large saccular body of this nature on the right side of the body. It has been suggested that the neural gland plays a part in renal excretion.

Reproductive Organs. The Tunicata are with very few exceptions (e.g. *Oikopleura dioica*) hermaphrodite, and as a general rule the female organ ripens first. So far as can be ascertained the gonads have no relations with the coelom, either developmentally or otherwise. The glands are continuous with

* Schultze, *Jena Zeitsch.*, 35, 1901, p. 221.

† Dahlgrün. *Arch. f. mik. Anat.* 58, 1901, p. 608

their ducts, the terminal parts of which are usually single and open into the atrial cavity. The ovaries and testes are generally placed near one another and contained either amongst or near the digestive viscera or in the mantle wall. In the *Polyclinidae* they are in the post-abdomen. In *Ciona* (Fig. 13) the testis is a branched gland ramifying on the wall of the intestine between the pylorus and the rectum. Its tubules gradually collect into one main duct, which accompanies the rectum and opens into the atrium in front of the anus by several openings, the walls of which contain a red pigment, consisting of red renal vesicles of the kind referred to above. The ovary is a rounded mass placed in the intestinal loop, and the oviduct accompanies the vas deferens to open close by it, far forward into the atrium.

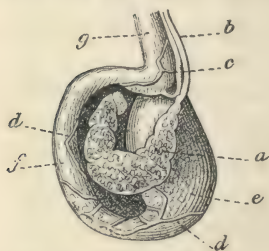


FIG. 13.—Intestinal loop and genital organs of *Ciona intestinalis* (from Vogt and Yung).
a ovary; b oviduct; c vas deferens; d testicular tubes ramifying on the gut-wall; e stomach; f intestinal loop; g rectum.

The gonads arise from a common mesodermal rudiment. In the synascidians they do not as a rule appear in the zooid which develops from the egg, and they may be absent from the first-formed generation of budded zooids (*Botryllus*, etc.).

Reproduction by budding occurs in a large number of Tunicata. Sometimes, as in the synascidians, the budded individuals remain embedded in a common tunic with the parent; sometimes, as in *Thaliacea*, they become eventually separate and lead for a time an independent existence. In the latter case the life history is complicated by the phenomenon of alternation of generations of the variety known as metagenesis; for the individuals which bud proceed from the egg and do not develop sexual organs. Budding does not occur in the *Appendiculariae* and monascidians. In all cases excepting *Botryllus* the budding is effected by the division of a ventrally placed process of the body called the **stolon**. The stolon contains a diverticulum of the pharynx known as the **epicardium** and given off between the endostyle and the oesophageal opening (p 15). The stolon also contains an extension of the mesodermal and vascular tissues of the parent. For a more detailed account of the phenomenon and of the origin of the organs in the bud, we must refer the reader

to the accounts given below under each family or order. Here we will only remark that there is considerable variability in the mode of formation of the organs. The pharynx, atrium, digestive organs and pericardium are usually derived from the epicardial process of the pharynx, while the ganglion in the synascidians usually develops from the endoderm, but it may arise from the mesoderm (*Pyrosoma*) or from the ectoderm (Thaliacea). In the *Botryllidae* the endoderm of the parent does not participate in the budding process.

Development. In most monascidians (except *Cynthia*, etc.) the eggs are fertilised in the sea or in the atrium and undergo their whole development outside the body of the parent. This is also the case in *Doliolum* and in the *Appendiculariae*. In the synascidians on the other hand the early development usually takes place in the atrial cavity or in incubatory pouches of it. In the salps the egg undergoes its early development in the ovary; in the later stages it emerges into the atrial cavity but remains connected with the parent by the placenta.

The eggs are frequently laid in their follicle, which is somewhat complicated. It is formed of two layers (Fig. 14), the outer of which consists of vacuolated cells; these are prolonged into papillae, and help to float the egg in the sea. The inner layer consists of follicle-cells which have migrated inwards, and are called the *test-cells* because formerly they were supposed to give rise to the test of the adult. The two layers are separated by a structureless chorion.

The development generally leads to the formation of a free-swimming tailed larva, the tadpole larva, by means of which the species is distributed over a wider area. The tadpole larva is nearly always formed in the monascidians (it is absent in some species of *Molgula*) and in the synascidians (absent in *Pyrosoma*). It is also found in *Doliolum*, but not in the salps.

The eggs usually have but little yolk. In the synascidians they are however richer in yolk, and in *Pyrosoma* the cleavage is actually meroblastic

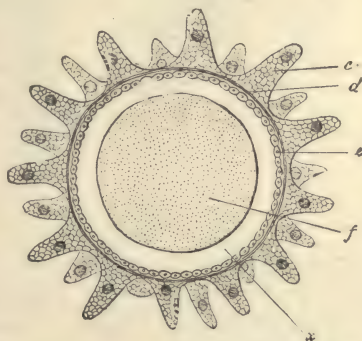


FIG. 14.—Mature egg from the oviduct of *Ciona intestinalis* (after Kupffer). *c* follicle cells (foam-like cells); *d* chorion; *e* test-cells; *f* ovum; *x* gelatinous substance.

Development of the tadpole larva. The segmentation is complete and leads to the formation of a blastosphere, from which the gastrula arises by invagination. The gastrula

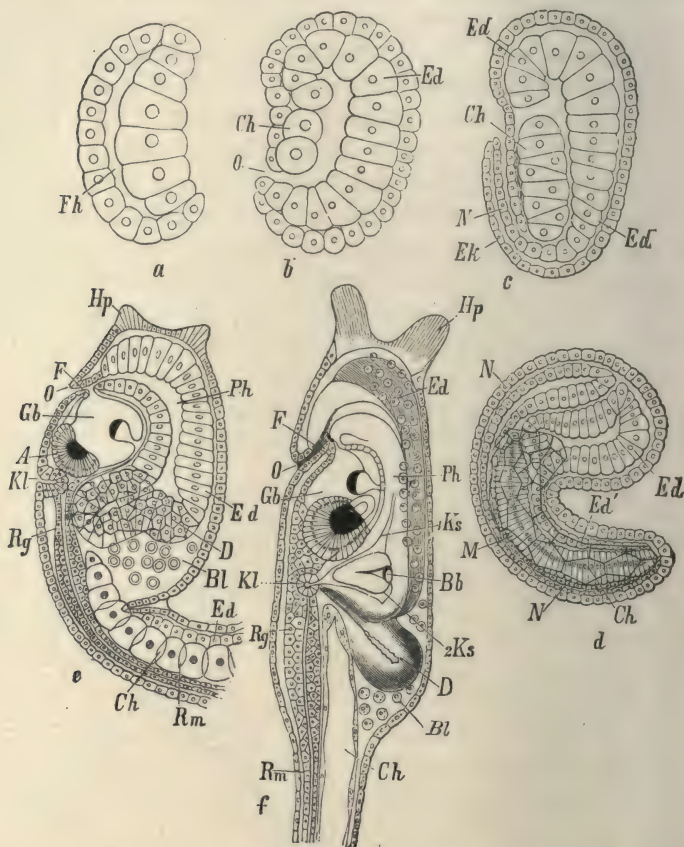


FIG. 15.—Development of *Phallusia mammillata* (after Kowalevsky from Claus). *a* Commencement of invagination; *fh* cleavage-cavity. *b* Gastrula with blastopore *O*; *ch* rudiment of notochord; *Ed* endoderm. *c* Later stage; *Ek* ectoderm; *N* rudiment of neural canal; *Ed'* endoderm of future tail region. *d* Stage with body and tail; *Ed'* endoderm of tail; *M* muscular cells in tail. *e* Just-hatched larva; *A* eye; *Bl* blood corpuscles; *D* commencing intestine; *Ed* endostyle; *F* opening of cerebral vesicle into mouth; *Gb* cerebral vesicle with otolith projecting from its floor; *Hp* papilla for attachment; *Kl* one of the atrial invaginations; *O* mouth; *Ph* pharynx; *Rg* anterior swelling of post-cerebral region of nerve tube; *Rm* posterior part of nerve tube. *f* Two days larva, only the anterior part of the tail is represented; *1 ks*, *2 ks* branchial stigmata; *Bb* blood sinus between them; *D* intestine.

elongates in the future antero-posterior axis and the blastopore comes to lie on the posterior end of the dorsal surface (Fig. 15 *b*). A flat median groove of ectoderm appears along the

dorsal side of the already bilaterally symmetrical embryo extending from the blastopore forwards. This groove, into the hind end of which the blastopore opens, is the first rudiment of the central nervous system. It is known as the medullary groove. Its edges project and form the medullary folds which grow round and close the narrow blastopore, and gradually unite with one another from this point forward in such a manner as to convert the groove into a canal, the walls of which separate from the external ectoderm and give rise to the central nervous system. This canal is the medullary canal; behind it is shut off from the exterior, but communicates with the cavity of the gastrula by way of the blastopore which is now called the neurenteric canal; while in front it remains open for some time, but eventually closes. Before these changes are completed, the medio-dorsal endoderm cells of that part of the gastric wall which immediately underlies the posterior part of the neural canal (Fig. 15, *c* and *d*, *Ch*) become different from the remaining endoderm cells and constitute the first rudiment of the notochord. Meanwhile the latero-dorsal endoderm, on each side of the notochord, has separated off the mesoderm as a solid * plate of cells (Fig. 16, *ms*). These, in the trunk, later become converted into a mesenchyme, occupying the space which now makes its appearance between the ectoderm and endoderm, and give rise to the blood-corpuscles, musculature, genital, and excretory organs of the body, while the caudal part becomes the musculature of the tail. The distinction between the caudal and trunk region of the embryo is now very apparent. The notochord is confined to the tail. The caudal part of the enteron becomes solid (Fig. 15 *d*, *Ed'*), though still remaining continuous with the medullary tube round the hind end of the notochord. Eventually it disappears, apparently giving rise to blood corpuscles.

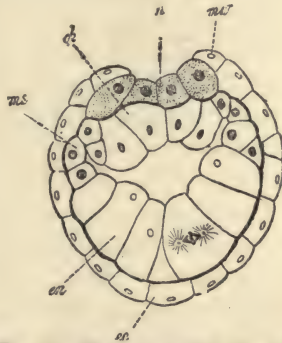


FIG. 16.—Transverse section through an embryo of *Clavelina* (after v. Beneden and Julin, from Korschelt and Heider). *ch* rudiment of notochord; *ec* ectoderm; *en* endoderm; *ms* rudiment of mesoderm; *mo* medullary folds; *n* medullary plate.

* According to van Beneden and Julin there is at first an enteric prolongation in the front part of this.

The anterior part of the enteron dilates and constitutes the rudiment of the pharynx (Fig. 15, *Ph*), from the hind end of which the intestine is developed as an outgrowth (*D*). In the further course of development the tail becomes greatly elongated and curved ventrally on the trunk (Fig. 15 *e*), and some ectodermal papillae are formed at the anterior end of the body for the future attachment of the larva (*Hp*). The anterior end of the medullary tube becomes dilated into the cerebral vesicle, in the wall of which two sensory structures—the eye and auditory organ—are developed (Fig. 15 *f*, *Gb*). The part of the medullary tube immediately behind this acquires thickened walls and is called the trunk ganglion (*Rg*). This is followed by the narrow caudal extension of the tube which ultimately disappears. The mouth is formed as a perforation on the dorsal surface of the front end and the cerebral vesicle acquires an opening into the anterior part of the alimentary canal (Fig. 15 *f*, *o*). The atrium arises as two dorso-lateral invaginations of ectoderm (*kl*) into the left of which the anus opens. The atrial invaginations spread laterally round the pharynx but remain separate ventrally; dorsally they coalesce, so that the single atrial aperture arises. The gill-slits or branchial stigmata arise as a pair of perforations of the wall separating the atrial cavity from the pharynx. They subsequently become more numerous, partly by formation of new perforations and partly by division of those already existing. The endostyle arises as a groove on the anterior (Willey) or antero-ventral wall of the pharynx, but subsequently, as a consequence of the rotation which the body undergoes at the metamorphosis (Fig. 18), becomes entirely ventral.

The development of the *epicardium*, which as we have seen above is probably to be regarded as the coelom of the animal, seems to take place in different ways in different forms. In *Ciona* it arises from the hind end of the pharynx as two diverticula which remain separate throughout life and invest the digestive viscera like a perivisceral cavity. In *Clavelina* (Fig. 17, *ep*) it appears to arise as a single diverticulum of the pharynx between the end of the endostyle and the oesophagus, the front end of which becomes double. In some cases however it is apparently delaminated from the pharynx and is at first solid. The pericardium in a great number of cases, if not universally, is nipped off from the epicardium either from its posterior unpaired portion

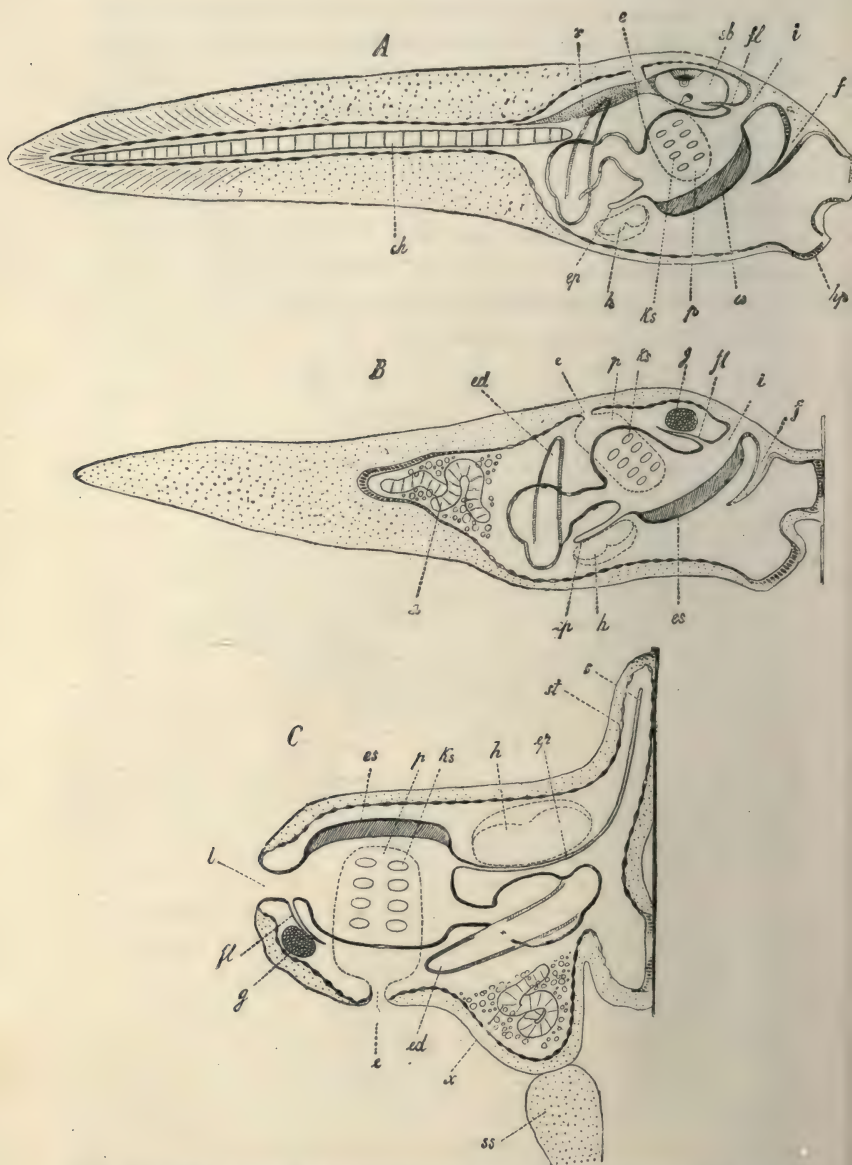


FIG. 18.—Diagram illustrating the metamorphosis of the larva of *Clavelina* during and after fixation (from Korschelt and Heider, after Seeliger). A Free-swimming larva. B Larva just attached. C Older metamorphosed stage. *ch* notochord; *e* atrial aperture; *ed* intestine; *ep* epicardium; *es* endostyle; *f* ectodermal fold; *fl* duct of neural gland; *g* ganglion; *h* heart; *hp* adhesive papillae; *i* mouth; *ks* gill-slits; *p* atrial cavity; *r* trunk-ganglion; *s* partition wall of stolon; *sb* cerebral vesicle; *ss* cast cellulose tissue of tail; *st* stolo prolifer; *x* larval tail degenerating.

not take place, the animal remaining throughout life attached by a stalk which arises close to the mouth (Fig. 19, 2).

The following classification has been adopted :—

Order 1. Ascidiacea.

Tribe 1. *Ascidiae simplices*, **Monascidia**.

„ 2. *Ascidiae compositae*, **Synascidia**.

„ 3. *Ascidiae salpaeformes*, **Ascidiae Luciae**.

Order 2. Thaliacea.

Sub-order 1. **Hemimyaria, Salpida**.

„ 2. **Cyclomyaria, Doliolida**.

Order 3. Appendiculariae (Perennichordata, Larvacea, Cope-lata).

Order 1. ASCIDIACEA (TETHYODEA).

Fixed or free-swimming, solitary or colonial Tunicata, which in the adult are never provided with a tail and have no trace of a notochord. The free-swimming forms are colonies and the solitary forms are fixed.

The test is permanent and well developed ; as a rule it increases with the age of the animal. The musculature of the mantle is in the form of an irregular network, there being no regular circular bands. The pharynx is large and well developed. Its walls are perforated by numerous apertures opening into a single atrial (peribranchial) cavity, into which the anus opens and which communicates with the exterior by an atrial aperture. The colonial forms reproduce by gemmation, and in most the sexually produced embryo develops into a tailed larva. The order is divided into three groups, the *Ascidiae Simples*, the *Ascidiae Compositae* and the *Ascidiae Salpaeformes*.

These three groups can only be regarded as tribes, for they are closely interrelated, and are distinguished, the two first by the presence or absence of the power of budding and the last by being free-swimming. If other and more general anatomical characters were taken, quite a different grouping of the families would be obtained, and there can be no question that some of the families of synascidians are more closely related to certain families of the monascidians than to each other. But if in the grouping of the families account were taken of these facts it is difficult to say that a more natural system of classification would be obtained ; cross-relationships between the groups constituted would still exist, and would by many be considered to be of sufficient importance to justify a different

grouping, so that it seems best to adopt a plan which has at least the merit of being simple and easy of application.

Tribe 1. ASCIDIÆ SIMPLICES (MONASCIDIA).

Solitary usually fixed forms, incapable of budding in the adult state ; with large pharynx, and numerous branchial stigmata.

These are the typical sea-squirts. They are solitary forms usually of considerable size and attached by their tunics to rocks and sea-weeds. A few however, e.g. *Molgula*, are not attached save to grains of sand by processes of the test, and in a few stalked forms the stalk arises from near the mouth (*Boltenia Culeolus*, Fig. 19). The tunic is usually somewhat thick and opaque and may have a cartilaginous consistency. When touched they frequently discharge two streams of water which proceed from the two openings, the one, the mouth or inhalent opening which is terminal and at the free end, the other the cloacal or atrial aperture, which is placed on the dorsal surface a little distance from the free end. The protective covering of mud or sand is generally associated with fibrous processes of the test (*Molgulidae*, *Polycarpa molguloides*, *Ascidia conchilega*), but in some cases the sand adheres directly to the test.

In *Culeolus*, *Fungulus* and *Bathyoncus*, abyssal forms belonging to different sub-families of the *Cynthiidae*, the pharynx presents the remarkable modification of being without the fine longitudinal bars (Fig. 20). The dorsal lamina varies from the condition of a membrane to that of a series of languets ; an intermediate condition of a toothed membrane being found.

The viscera are placed in the body-wall at the level of the hinder part of the pharynx (except in *Ciona*), usually on the left side. They project into the atrial cavity, sometimes being attached to its wall by a mesentery. The atrial cavity is always traversed by vascular strands passing from the pharynx wall to the mantle wall. The vascular system is well developed, the sinuses sometimes having the aspect of vessels. There is usually a tailed larva.

Fam. 1. Ascidiidae. Usually sessile, rarely pedunculated ; mouth usually with 8 lobes, atrial aperture with 6 ; pharyngeal wall without folds, with internal longitudinal bars bearing papillae ; stigmata straight or curved ; tentacles unbranched ; gonads placed in the intestinal loop. *Ciona* approximates to the Clavelinidae by the position of its viscera and the presence of an epicardium (pp. 15, 37).

Pharynx with internal longitudinal bars and straight stigmata, viscera on the left side of pharynx, dorsal lamina as a membrane.

Ascidia L. (Figs. 2, 12), test soft, *A. mentula* O.F.M.; *Phallusia* Sav., *P. mammillata* Cuv., pharynx recurved on itself posteriorly on the left side, Seas of Eur.; *Pachylaena* Herd., test hard.

Pharynx as above, dorsal lamina as languets.

Ciona Flem. (Figs. 1, 3, 4, 6A, 11, 13, 14), viscera posterior to pharynx, tunic gelatinous, renal cells grouped near the generative orifice, *C. intestinalis* L. most seas. *Rhodoma* Ehrenberg (*Chevreulius* L.-Duth.) (Fig. 19), test folded at the anterior end so as to form a kind of bivalve operculum covering the mouth and atrial opening, viscera on right side, Med. *Abyssascidia* Herd., attached by ventral surface, apertures far apart, deep-sea, 2,000 to 2,600 fms., viscera on either right or left side of pharynx.

Pharynx with

internal longitudinal bars, curved stigmata and viscera on right side of pharynx, dorsal lamina as languets.

Corella Ald. and Han., test soft, seas of Eur., Japan etc. *Chelyosoma* Brod. and Sow., test modified into horny plates. *Corynascidia* Herd., as above, but with viscera dorsal to pharynx and a stalk, deep sea, 1,000 to 2,000 fms.

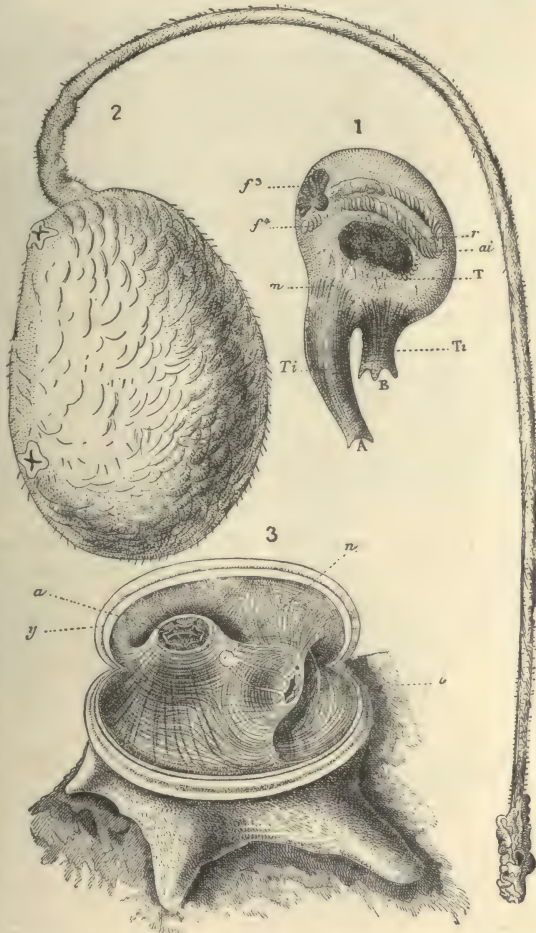


FIG. 19.—1. *Molgula* (*Anurella*) *solenota*, from the right side (nat. size). *A* atrial pore, *B* mouth, at the end of papilliform prominences. *Ti*, *Ti*; *ai*, *r* alimentary canal; *f*³, *f*⁴ liver; *T* reproductive glands. 2. *Boltenia oviformis* × $\frac{1}{2}$. 3. *Rhodoma* (*Chevreulius*) *callense* × 3; *a* mouth; *n* ganglion; *o* atrial aperture; *y* operculum (from Ferrier).

Pharynx without internal longitudinal bars, stigmata small and irregular, dorsal lamina as a membrane, viscera on dorsal edge of pharynx.

Hypobythius Moseley, stalked, test thickened in places to form plates, 600 to 3,000 fms.

Fam. 2. **Cynthiidae**. Usually attached, rarely free, sometimes pedunculated; mouth aperture usually 4-lobed, atrial 4-lobed; pharyngeal wall longitudinally folded, internal longitudinal bars without papillae, stig-

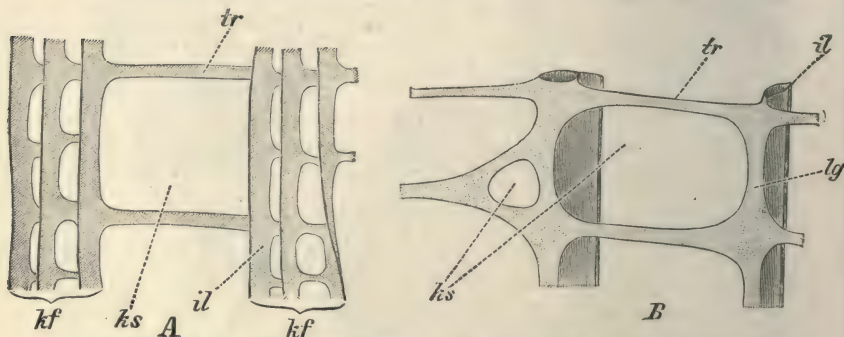


FIG. 20.—A Portion of the pharyngeal wall of *Bathyoncus mirabilis*, B of *Culeolus wyville-thomsoni* (from Bronn, after Herdman). *il* inner longitudinal bar; *kf* folds of pharyngeal wall; *ks* pharyngeal apertures; *lg* longitudinal bars; *tr* transverse bars.

mata straight; tentacles simple or branched; intestine on the left side, only slightly or not at all attached to the mantle; gonads on the inner surface of the mantle, either on both sides or on one only. In the genera *Culeolus*, *Cystingia* and *Fungulus*, etc., the stigmata are large and quadrangular, and fine longitudinal bars are supposed to be absent (Fig. 20). It is doubtful however if this interpretation is correct (see p. 12).

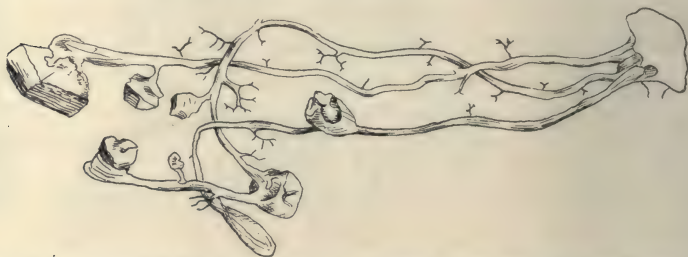


FIG. 21.—Filaments of the tunic of *Molgula roscovita*, showing the swellings to which the grains of sand are attached (from Delage and Hérourard, after L.-Duthiers).

Sub-fam. 1. **Bolteninae**. Pharynx with more than 4 folds on each side; tentacles compound; body on a long stalk. *Boltenia* Sav. (Fig. 19), pharynx wall with the fine longitudinal bars, stalk arises on ventral surface near mouth, N. Atlantic, Australasia, Arctic. *Cystingia* MacLeay, the transverse and longitudinal bars of the pharynx form a loose meshwork, fine longitudinal bars absent, Arctic. *Fungulus* Herd., pharyngeal walls with square meshes, no fine longitudinal bars, stalk short and thick, dorsal lamina as a membrane, abyssal

forms. *Culeolus* Herd., without fine longitudinal bars (Fig. 20), stalk long and thin, dorsal lamina as languets, calcareous spicules in the connective tissues in the walls of the endostyle, pharynx, tentacles, etc., abyssal forms.

Sub-fam. 2. **Cyn-**

thiinae. Sessile or shortly pedunculated, pharynx with more than 4 folds on each side (except *Forbesella*), tentacles branched. *Microcosmus* Heller. *Rhabdocynthia* Herd., spicules in the tunic and connective tissues, S. hemisphere. *Cynthia* Sav., spicules in the test, mantle and pharynx, in most seas. *Forbesella* Herd., pharynx with 4 folds on each side, Eur.

Sub-fam. 3.

Styelinae. Sessile, rarely incrustated with sand; pharynx with 4 or less than 4 folds on each side; tentacles unbranched, development usually in an incubatory cloacal pouch. *Styeloides* Sluiter, pharynx and alimentary canal absent (Willey has shown that this is due to eviscerations, *Q.J.M.S.*, 39, p. 145), Malay Arch. *Pelonaia* Forbes and Goodsir, without folds in

pharynx. *Styela* MacLeay, pharynx with 4 folds or less, most seas. *Styelopsis* Traustedt, pharynx with one fold on the right side, gonads on right side only, Eur. *Bathyoncus* Herd., pharynx without stigmata and fine longitudinal bars (Fig. 20), abyssal form. *Dendroda* MacLeay, *Glandula* Stimp., *Polycarpa* Heller, sometimes covered with

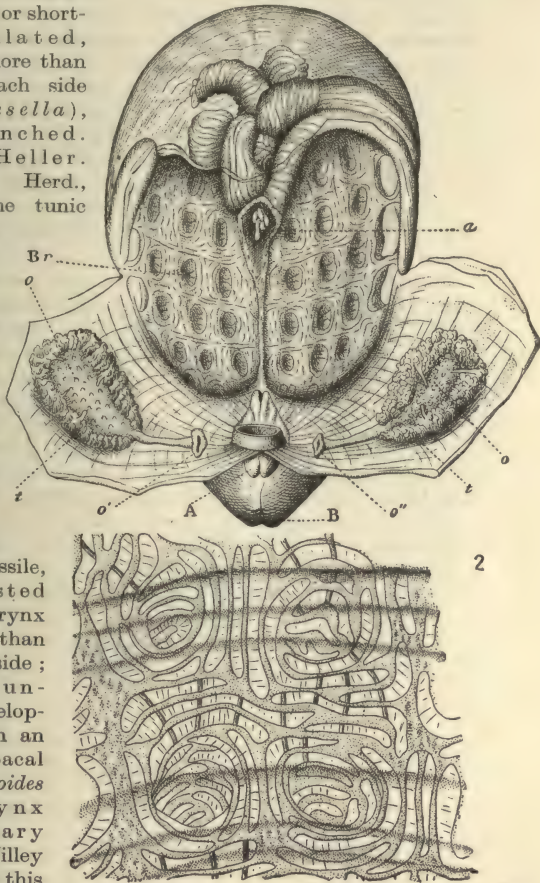


FIG. 22.—*Molgula roscovita*. 1. The mantle has been opened on the dorsal side to show the pharynx *Br* and genital glands. *A* atrial aperture, *a* anus; *B* mouth; *Br* pharynx; *o* ovary; *o'* opening of oviduct; *t* testis. 2. Portion of pharynx wall of *Molgula echinosiphonica*, showing the complication of the stigmata (from Perrier, after L.-Duthiers).

sand, rarely pedunculated, pharynx with 4 or less than 4 folds on each side, gonads in the form of a number of small separate masses scattered over the inner surface of the mantle, calcareous spicules in connective tissue of the mantle, most seas.

Fam. 3. **Moigulidae**. Usually free, sometimes fixed, rarely stalked; test usually covered with sand adherent to long, hair-like processes of the test (Fig. 21); mouth 6-lobed, atrial aperture 4-lobed; dorsal tubercle extremely variable, being circular, slightly spiral, and largely spiral within the limits of a single genus; pharynx wall usually longitudinally folded* (5-7 folds on each side), internal longitudinal bars without papillae, stigmata more or less curved, usually arranged in spirals (Fig. 22); tentacles usually much branched, of two or three regularly alternated sizes; intestine attached to inner surface of mantle on left side; renal organs aggregated in a sac upon the right side; gonads on inner surface of mantle, usually paired (Fig. 22); larvae anurous in a few species.

Molgula Forbes (Fig. 19), apertures not laciniated, pharynx with 6 or 7 folds, most seas. *Anurella* L.-Duthiers, very similar, larvae anurous. *Gymnocystis* Giard. *Pera* Stimpson, pharynx with 5 folds, Atlantic and Arctic. *Ascopera* Herd., stigmata not in spirals, lobes of the apertures plain, abyssal, test without processes, stalked, Kerguelen. *Ctenicella* L.-Duthiers, apertures laciniated, Med. *Eugyra* Alder and Hancock, pharynx not folded, but with saccular diverticula in longitudinal rows, gonads unpaired, most seas. *Paramolgula* Traustedt, pharynx without folds, stigmata spirally coiled and in infundibula, gonads paired. *Bostrichobanchus* Traustedt; *Gamaster* Pizon. *Oligotrema* Bourne, New Britain.

Tribe 2. ASCIDIAE COMPOSITAE (SYNASCIDIA) †

Fixed (except Coelocormus) colonial forms, the individuals of which reproduce by gemmation and are embedded in a common test (except Clavelinidae).

The embryos usually undergo their development in the atrial cavity or in a special incubatory pouch which they do not leave until they have developed into the tailed larva.

Fam. 1. **Botryllidae**. Colony usually thin and encrusting, sometimes in the form of thick fleshy masses; zooids arranged in systems (Fig. 23) circular or elliptical or in branching lines, the zooids of a system opening into one common cloaca; common cloacal openings distinct, usually lobed: zooids short, not divided into regions, disposed almost tangentially to the surface of the colony; intestine on the left side of the posterior part of

* The folds are really longitudinal rows of saccular projections (*infundibula*) of the pharyngeal wall into the peribranchial cavity.

† Pizon, Histoire de la blastogénèse chez les Botryllidés, *Ann. Sci. Nat.* (7), 14, 1893. *Id.*, Embryogénie de la larve double des Diplosomides, *Compt. Rend.*, 1893. *Id.*, Etudes biologiques sur les Tuniciers Coloniaux fixés, *Bull. Soc. Ouest France*, 10, 1900. Hjort, Ueb. d. Entwicklungs-cyclus der zusammengesetzten Asciden, *Naples Mit.* 10, 1893, p. 584.

the pharynx ; test usually soft, with numerous vessels ending in terminal knobs and joined to the body of each zooid at two points ; pharynx large with 3 internal longitudinal bars on each side and numerous stigmata ; dorsal lamina as a membrane ; tentacles simple, not more than 16 ; gonads on both sides in the mantle (except *Symplegma*) ; gemmation lateral, from the bodies of the zooids* ; the neural gland is dorsal to the ganglion in *Botryllus* ; the stomach has an hepatic caecum.

The budding of *Botryllus* differs from that of other synascidians in that the endoderm does not participate ; the bud being formed as an outgrowth of the atrial cavity and consisting only of outer ectoderm of the body, ectodermal lining of the atrial cavity and interposed mesoderm (Fig. 24). The process begins in the larva before hatching, as a pair of ventral outgrowths of the atrial cavity. After fixation of the larva the left of these atrophies and the right alone develops. The zooid produced from it gives rise to two buds by a process which is described below and is repeated in all the subsequent budding. The zooids of the colony thus increase in geometrical ratio, but in all cases when the buds are developed, the form which has produced them dies ; thus the fixed larva dies when it has produced its bud, and the latter dies when it has developed and produced its two buds. The zooids produced arrange themselves so that their atrial cavities are turned towards one another and open into the common cloaca which is a depression of the surface of the colony as in *Pyrosoma*. A system of zooids thus arises. The number of zooids in a system is limited ; when the limit is reached, of the two buds which each zooid produces one atrophies, and the other, instead of taking up its position in the system, moves away from it and becomes the centre of a new system in the same colony. The budded zooids do not separate from the parent as in most synascidian colonies. It is true that the pharynx of the bud loses its connection with the atrium of the parent, but the outer ectodermal connection persists and becomes an elongated and slender tube by which the vascular systems of the parent and bud remain in continuity. On the atrophy of the parent zooid the two tubes which connected her to her offspring become directly continuous owing to the fact that though the internal organs of the parent break down, its ectoderm persists.

As stated above the buds are formed as diverticula of the atrial cavity on its ventral side (Fig. 24). They form hollow vesicles, the cavity of each of which divides into two ; one of these becomes the pharynx and the

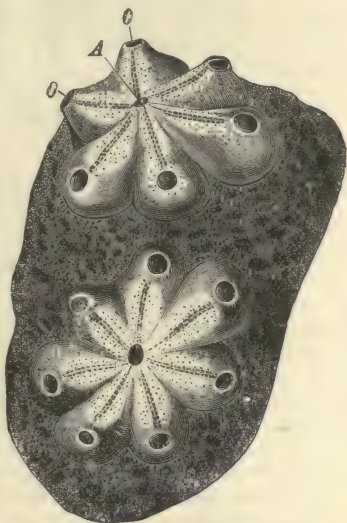


FIG. 23.—*Botryllus violaceus* (after M. Edwards from Claus). O mouth ; A opening of common cloaca of a system.

* In *Sarcobotrylloides* Herdman describes stolonial budding from the vessels of the test.

other, saddle-shaped, becomes the atrium of the bud. The organs are formed in the usual way, the pericardium and intestine as outgrowths of the pharynx and the nervous system from the endoderm. The original connection remains throughout life as the vascular ectodermal tube referred to above.

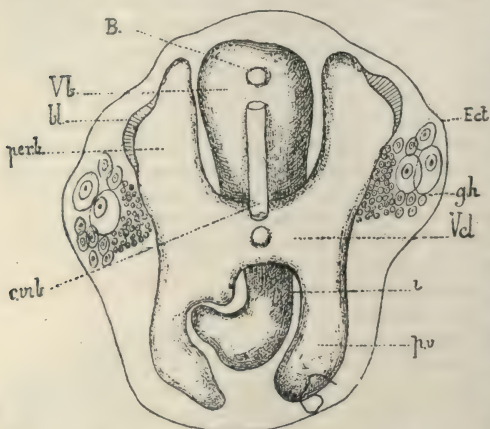


FIG. 24.—Diagram of a dorsal view of a young oozoid or of a bud of *Botryllus violaceus* (after Pizon, from Perrier). *B* future mouth; *vl* rudiment of new blastozooid of one side; *c.vib* vibratile tube; *ect* ectoderm; *gh* gonad; *i* intestine; *perib* peribranchial sac (atrial cavity); *pv* epicardial diverticulum; *vb* pharynx; *Vcl* cloacal part of future atrial cavity.

Drasche, like last, but colony thick and fleshy. *Symplegma* Herdman, colony stalked, gonads unpaired, in intestinal loop, Bermuda.

Fam. 2. **Distomidae.** Colony rounded or massive, rarely encrusting, either sessile or with long peduncle; systems irregular, inconspicuous or absent, both mouth and atrium usually opening on the surface of the colony. Zooids divided into thorax and abdomen, and sometimes provided with long vascular ectodermal appendages; test gelatinous or cartilaginous, sometimes with non-stellate calcareous spicules; pharynx without internal longitudinal bars; dorsal lamina as languets; gonads and heart in or alongside intestinal loop, spermatid vesicles numerous, vas deferens straight.

In the *Distomidae* the budding is epicardial. The epicardium arises as a pair of diverticula of the pharynx, one on each side of the oesophagus. The right of these detaches a pericardium, then separates from the pharynx and becomes connected to the left tube to form the definite epicardial tube. This pushes out the ectoderm and forms a ventral stolon, which buds off small free bodies into the test; these may multiply by fission and eventually develop into new zooids.* In *Colella* some of the buds, those placed in the deeper parts of the stalk, have a store of reserve food material in their ectoderm.



FIG. 25.—*Distaplia* (after Herdman from Delage and Hérouard).

* Kowalevsky, *op. cit.* Julin, *Int. Cong. Zoology*, Leyden, 1896.

Distaplia Della Valle (Fig. 25), with a common cloaca and atrial languets, incubatory pouch as diverticulum of cloaca, colony sessile or only shortly pedunculated; Med., Atl., Ind. Ocean. *Julinia* Calman, Antarctic. *Distoma* Gärtner, with atrial siphon, without spicules in the test and incubatory pouch, colony sessile or only shortly pedunculated; Med., Eur., Torres Straits. *Heterotrema* Fiedler, *Cystodites* v. Drasche, *Colella* Herd., with an incubatory pouch and a well-marked peduncle, S. Ocean. *Oxycornia* v. Drasche. *Chondrostachys* Macdonald, the zooids project beyond the test, Aust. *Archidistoma* Garstang, the zooids arise from an incrusting basal layer, either singly or united in a common test, without common cloaca; covered with sand; may be compared to a *Clavelina* in which the tests of the zooids have fused in groups; Plymouth.

Fam. 3. **Polycliniidae.** Colony usually massive, sometimes encrusting, sometimes lobed or even stalked; systems of various shapes, sometimes irregular or absent; common cloacal apertures usually indistinct or absent; zooids placed perpendicular to surface, usually divided into thorax, abdomen, and post-abdomen (Fig. 26); mouth 6 or 8-lobed, atrial aperture often

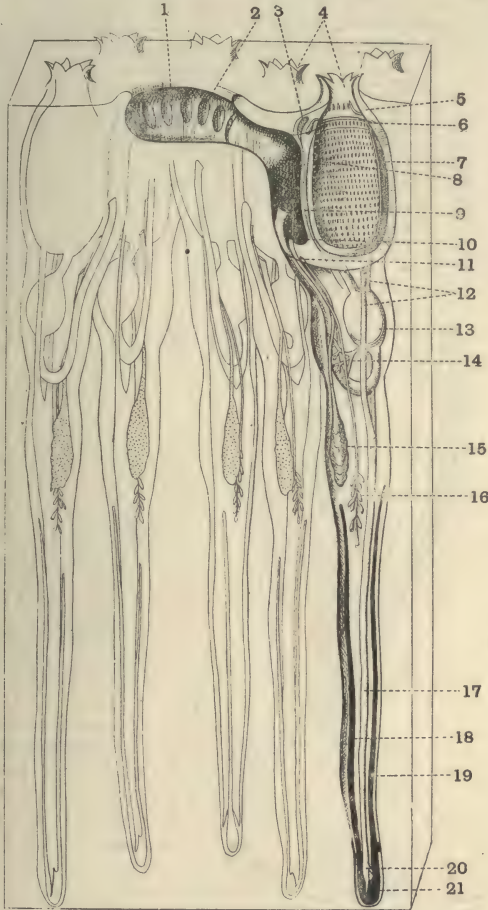


FIG. 26.—Diagrammatic section through a portion of a Polyclinid colony (after Delage and Hérouard). 1 opening of common cloaca; 2 atrial openings; 3 ganglion; 4 mouths; 5 tentacles; 6 peripharyngeal band; 7 endostyle; 8 languets; 9 anus; 10 male; 11 female generative opening; 12 epicardial tubes; 13 stomach; 14 pyloric gland; 15 ovary; 16 testis; 17 epicardium; 18 dorsal; 19 ventral limb of pericardium; 20 posterior bifurcation of epicardium; 21 heart.

with atrial languet; test sometimes stiffened by embedded sand grains; pharynx small with small stigmata, without internal longitudinal bars, with horizontal membranes; tentacles small, few; dorsal lamina as languets; gonads in post-abdomen, testis as spermathecae attached to

large vas deferens; gemmation from post-abdomen which has the heart at its extremity.

The post-abdomen contains the epicardium, which divides it into a right and left portion, the heart and pericardium, and in its upper part the gonads (Fig. 26). The pericardium (19) is U-shaped and contains the heart (also U-shaped) in its posterior part. The epicardium (17) bifurcates in front into two tubes which abut against the pharynx but do not open into it in the adult; posteriorly it bifurcates so as to grasp the bend of the pericardium (20). Budding is effected by the separation of the post-abdomen from the abdomen and its fission into pieces (Fig. 27). The portion of the heart and pericardium in each piece atrophies and the epicardium develops in the usual way into pharynx, atrium and intestine of the bud. In *Amaroucium*, and possibly others, budding takes place in the summer; towards winter this ceases and sexual organs are formed. The budding zooid regenerates a new post-abdomen. This method of budding is clearly of the stolonian kind, such as we find in *Clavelina* and *Distomidae*, differing only by the presence of the heart in the stolon.

With intestinal loop twisted and generally smooth-walled stomach.

Polyclinum Sav. (Fig. 26). Systems simple, stomach smooth-walled, most seas. *Glossophorum* Lahille, horizontal membranes of pharynx denticulated, each colony of a single system; Med. *Aptogaster* Herd., *Polyclinoides* v. Drasche, *Aplidiopsis* Lahille, with non-twisted intestine and smooth-walled stomach; Med., Atl. *Pharyngodictyon* Herd., pharynx with simple

meshwork of rectangular meshes, fine longitudinal bars supposed to be absent (see p. 11); Antarctic, 1,600 fms.; *Tylobranchion* Herd.

Intestinal loop not twisted, wall of stomach grooved or areolated.

Apilidium Sav., without languets, most seas. *Psammopilidium* Herd. *Amaroucium* M.-Edw. (*Amaroecium*) (Fig. 27), atrial aperture with a languet, post-abdomen not separated off by constriction, most seas. *Sigillina* Sav., *Fragarium* Giard and *Fragaroides* Maur., with 8 buccal lobes, Med. *Sidnyum* Sav., 6 buccal lobes, areolated

FIG. 27.—*Amaroucium* showing segmented post-abdomen, *x*, *y* buds, *k* anterior swollen end of epicardium in the bud (after Kowalevsky).

stomach; N. and S. Atl. *Morchellium* Giard. *Synoeicum* Phillips, each colony forms a separate club-shaped mass. *Parascidia* M.-Edw. *Circinalium* Giard. *Morchellioides* Herd. *Polyclinopsis* Gottschaldt.

Fam. 4. **Didemnidae**. Colony usually thin and encrusting, rarely thick, never stalked; systems irregular, inconspicuous or absent, common cloacal apertures usually conspicuous; zooids placed perpendicularly or obliquely to surface, divided into thorax and abdomen; mouth 6-lobed, atrial opening plain or with atrial languet; test usually with stellate calcareous spicules; ectodermal processes well developed, with muscles which

act as retractors; pharynx small, with 3 or 4 (rarely 6) rows of stigmata; gonads alongside intestinal loop, ova large, single testis round which vas deferens is coiled spirally; gemmation from pyloric region, thorax and abdomen formed from separate buds; larval gemmation feeble.

The budding* (Fig. 28) in the *Didemnidae* is very remarkable. The buds appear to arise in two separate portions from distinct parts of the body; the one of these, known as the *thoracic bud* (*b*), arises as a diverticulum of the outer wall of the lower end of the atrial cavity, on the right side opposite the stomach; the other, called the *abdominal bud* (*c*), is a diverticulum of the oesophagus which also projects towards the right side. The thoracic bud is formed of outer ectoderm, ectodermal lining of the atrial cavity and interposed mesoderm (like the bud of the *Botryllidae*); it gives rise to the thoracic portion of a new zooid, *i.e.* to the pharynx, atrial cavity, rectum and a portion of the oesophagus (Fig. 28, *B*). It separates from its place of origin and acquires new relations; these are as follows: the mouth opens on the surface of the colony, the atrial aper-

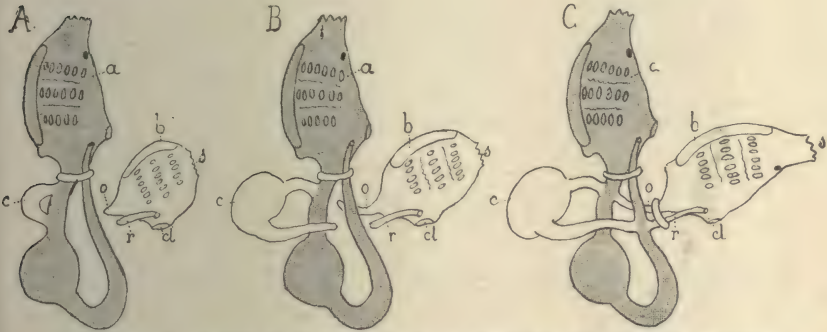


FIG. 28.—Three successive stages in the budding of *Didemnum* (from Delage and Hérouard, 1, after D. Valle). *a* parent; *b* pharyngeal bud; *c* abdominal bud; *cl* atrial aperture; *O* oesophagus; *r* rectum; *s* mouth of bud.

ture into the common cloaca of the colony, the portion of oesophagus joins the oesophagus and the rectum joins the rectum of the parent. The abdominal bud meanwhile has formed itself into a loop connected at both ends with the oesophagus of the parent; one end however separates itself from the oesophagus, joins the rectum close to the point of union of the latter with the rectum of the thoracic bud; and the whole loop forms itself into a new oesophagus, stomach and intestine. A new heart and pericardium are formed in the abdominal bud. Later when the new pharynx and new intestine have developed so as to be equal in size to those of the parent, they become detached from its oesophagus and rectum and join up in such a way that the oesophagus and rectum of the abdominal bud become continuous with the oesophagus and rectum of the thoracic bud. Such is this extraordinary phenomenon. The details are not yet fully worked out, and we await future observations for a more complete understanding of it. It sometimes happens that the two parts of the bud are not equally

* Della Valle, *Mem. R. Accad. Lincei* (3), 10, 1881, and *Arch. Ital. Biologie*, 3, 1883. Caulery, *Comp. Rend.*, 1895-97. Salensky, *Naples Mit.*, 11, 1895.

developed, or one part alone may develop, so that zooids may be found with two sets of intestines. In such cases the old intestines disappear and the phenomenon may be regarded as one of regeneration.

Didemnum Sav., colony thick and fleshy, pharynx with three rows of stigmata, most seas. *Didemnoides* v. Drasche. *Sarcodidemnoides* Oka. *Leptoclinum* M.-Edw., colony thin and encrusting, 4 rows of stigmata. *Tetradidemnum* Della Valle. *Polysyncrator* Nott. *Eucoelium* Sav., 6 rows of stigmata, Med. and Red Sea. *Hypurgon* Sollas, with faecal pellets included in the test, Malay Peninsula.

Fam. 5. **Diplosomidae.** Colony usually thin, transparent and encrusting, usually without spicules in the test, pharynx with 4 rows of stigmata; body divided into thorax and abdomen; vas deferens not spirally coiled; gemmation* as in the *Didemnidae*; the larva produces a well-developed bud before fixation. *Diplosoma* Macdonald, Med., Atl., Pac., Austr. *Diplosomoides* Herd., with spicules, Med. *Brevistellium* Jourdain. *Asstellium* Giard. *Pseudodidemnum* Giard.

Fam. 6. **Coelocormidae.** Colony massive, deeply concave on upper surface, not attached; zooids large, scattered all over the surface, mouth 5-lobed; test soft with calcareous spicules near surface of colony; pharynx large, dorsal lamina as languets; intestine extending behind pharynx but not forming distinct abdomen; testis as pyriform vesicles which join a spirally coiled vas deferens. *Coelocormus* Herdman, S. Atlantic, 600 fms.

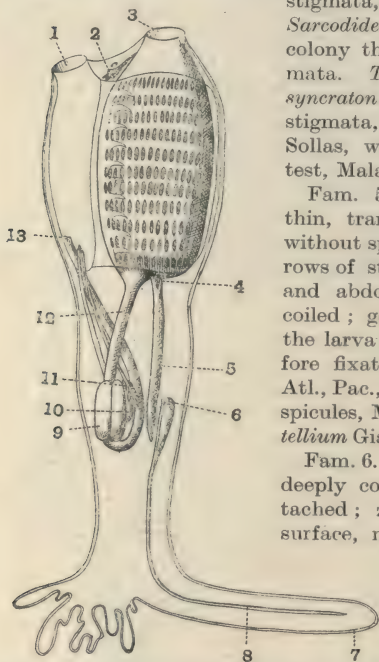


FIG. 29.—A blastozooid of *Clavelina*, side view, diagrammatic (after Delage and Hérouard), 1 atrial aperture; 2 subneural gland; 3 mouth; 4, 5, epicardial tube; 6 heart; 7 stolon; 8 stolon; 9 stomach; 10 ovary; 11 testis; 12 oesophagus; 13 anus.

* From the recent account of Pizon (*Comptes Rendus*, 137, 1903. p. 759) which is somewhat condensed, the budding appears to be as follows:—The larva buds before fixation. Of the two individuals so formed, O¹ and B¹, the oozoid O¹ or zooid into which the larva itself develops buds a new thorax (pharynx, oesophagus and rectum) and so becomes *bithoracic*. After twenty-four hours the old thorax degenerates, while its abdomen V¹ persists and retains its connection with the budded thorax. There is thus formed a new individual O², which in its turn produces two buds; from one of these proceeds a new thorax O³ from the other a new abdomen V². After about twenty-four hours these separate in such a way that the new thorax O³ takes the old abdomen V¹, while the thorax of O² keeps the new abdomen V². O² having thus acquired a new abdomen buds a new thorax O⁴ and then after twenty-four hours loses its old thorax. A new zooid with the old abdomen V² and the new thorax O⁴ is thus formed. O³ goes through the same series of changes as those described for O²; *i.e.* it first doubles itself and gives rise to two new zooids, of which that with the old thorax O³ becomes *bithoracic* and then loses its old thorax. The zooid B¹ produced by the free larva behaves like O².

Fam. 7. Polystyelidae. Colonies massive or encrusting, rarely stalked or formed of small masses connected by stolons, without common cloacal cavities; both apertures 4-lobed, opening directly to the exterior; pharynx large, with strong internal longitudinal bars; tentacles small, numerous; dorsal lamina as membrane; intestine alongside pharynx, rarely extending behind it; gonads as polycarps in mantle projecting into atrium; gemination doubtful, probably from vascular stolons; in *Goodsiria* it is stated to be pallial (Ritter). It is not certain that all the genera here included have the power of budding, and it is possible that some of them are close aggregations of simple Ascidians. By their structure they approach *Polycarpa* (*Styelinae*) of that group. *Goodsiria* Cunningham, *Chorizocormus* Herd., *Oculinaria* Gray, *Thylacium* Carus, *Polystyela* Giard, *Synstyela* Giard.

Fam. 8. Clavelinidae. The zooids are not embedded in a common test but are attached to creeping stolons or to a stolonial mass from which new ascidiozooids are formed by gemination; test usually gelatinous, thin and transparent; pharynx often without internal longitudinal bars, which are without papillae; tentacles simple, dorsal lamina as languets; intestine usually behind pharynx as abdomen; gonads in intestinal loop. This family comes closest to the genus *Ciona* of the simple Ascidians, with which group it is often united.

The stolon of * the oozoite of *Clavelina* (form produced from the egg) is divided into two parts by a septum, the *stolonial septum*. This is a collapsed continuation of the epicardium and therefore contains endoderm. At the free end of the stolon the septum ceases so that the cavities (blood spaces) on either side of it are in communication. At the other end the septum is continuous with the hind end of the single epicardial tube (in the blastozoote with the hind end of the pericardium, Fig. 29), the posterior part of which is applied to the dorsal side of the pericardium, while the front end forks to open by two openings into the hind end of the pharynx just ventral to the oesophagus. In the blastozoites or forms which have been produced by budding (Fig. 29), the arrangement is the same except that the stolonial septum is connected with the pericardium and not with the epicardium; but this is not a matter of any great importance, inasmuch as the pericardium develops from the hind end of the epicardium, with which it remains in close contact. The point is that the stolonial septum is an endodermal structure continuous with or developed from the pharyngeal wall. The form produced from the egg remains asexual, the zooids (blastozoites) which are budded from the stolon of this become sexual (Fig. 29). The budding takes place in this way. The stolon produces on its upper side a small diverticulum (Fig. 31), into which the septum sends a hollow endodermal prolongation. This

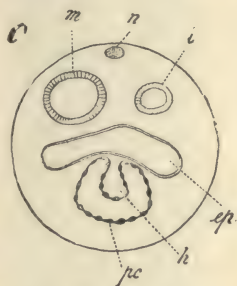


FIG. 30. — Diagrammatic transverse section through the posterior part of a bud of *Clavelina* (from Korschelt and Heider). *ep* epicardium; *h* heart; *i* intestine; *m* stomach; *n* visceral nerve cord; *pc* pericardial vesicle.

* Kowalevsky, Sur le bourgeonnement du *Perophora listeri*, *Rev. Sci. Nat. Montpellier*, 1874, and Ueb. d. Knospung d. Ascidien, *Arch. f. Mik. Anat.*, 10, 1874.

endodermal vesicle becomes constricted into two parts which remain connected by a narrow neck; the upper of these gives rise to the pharynx and atrial cavity, and the lower to the epicardium from which the pericardium subsequently proceeds. The digestive tube arises from the pharynx in the ordinary way, while the central nervous system appears to develop from the pharyngeal endoderm,* as it does also in the buds of

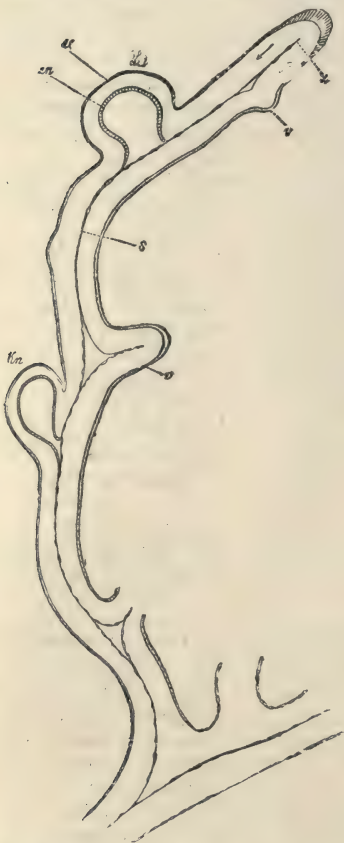


FIG. 31.—Portion of a proliferating stolon of *Perophora* (after Kowalevsky from Korschelt and Heider). *ec* ectoderm; *en* endoderm; *kn* buds; *s* stolon septum; *v* branching of the stolon.

Distaplia † and *Botryllus* ‡ and probably in those of all *Ascidiae Compositae*. It would thus appear that in the *Ascidiae Compositae* the atrial cavity and the central nervous system, which in the embryo develop from the ectoderm, in the bud develop from the endoderm. This contrast is highly remarkable, and due weight will have to be given to it, when we are considering in the General Part, the theory of the embryonic layers.

Clavelina Sav., stolons delicate and branched, body divided into thorax and abdomen, without peduncle, pharynx without inner longitudinal bars; 2–3 cm. in length; Eur. and Med. *Podoclavella* Herd., with peduncle, Arctic, Australia. *Stereoclavella* Herd., stolons and hind end of body in a common mass of test, Atlantic, Australia. *Pycnoclavella* Garstang, (*J.M.B.A.* (2), 2, 1891), similar to preceding, Plymouth. *Perophora* Lister, without abdomen, short peduncle, pharynx with 4 rows of stigmata, transverse bars of pharynx with papillae which branch and may form imperfect internal longitudinal bars (Fig. 8), zooids 3–5 mm.; Atl., Med., N. Amer., Austr. *Perophoropsis* Lahille, with 15 or 16 rows of stigmata, Med. *Ecteinascidia* Herd., without abdomen, test without blood-vessels, pharynx with internal longitudinal bars, most seas. *Sluiteria* v. Ben. *Diazona* Sav., many zooids united by

tests posteriorly to form a large colony, abdomen present and embedded in common test, pharynx with internal longitudinal bars, zooids 3–6 cm.

* Seeliger, *Z. f. w. Z.*, 56, 1893, p. 365–401. Ritter, *Journ. Morph.*, 12, 1896.

† Kowalevsky, *Arch. Mik. Anat.*, 10, 1874.

‡ Hjort, *Zool. Anz.*, 16, 1892, p. 328.

Eur. and Med. *Rhopalaea* Philippi, zooids few, not united by tests, stolons as foliaceous expansions ; 5-12 cm. ; Med. *Rhopalopsis* Herd.

Tribe 3. ASCIDIAE SALPAEFORMES (ASCIDIAE LUCIAE).

Free-swimming pelagic colonial Ascidians.

The colonies have the form of hollow cylinders, closed at one end, open at the other, and slightly tapering towards the closed end. The closed end is rounded ; the open end is flat and its edges project inwards to form a diaphragm (Fig. 32). The cavity of the cylinder is the common cloaca of the colony, and its opening, which can vary in size, is the common cloacal opening. The test is transparent and gelatinous ; it bears on its outer surface a number of projections (Fig. 31 *bis*), while the inner surface is perfectly smooth. The zooids are elongated antero-posteriorly and placed in the thickness of the wall of the cylinder in a single layer at right angles to the surface. Their mouths open on the outer surface, each at the base of one of the test processes ; and their atrial apertures are at the opposite end and open into the common cloaca. The colonies vary in length from a few inches to four feet (*Pyrosoma spinosum*). They float horizontally in the sea, and have a slight power of movement with the closed end forward. The movement appears to be caused by feeble longitudinal contractions of the wall of the hind end of the cylinder. They are phosphorescent. When they are at rest the light is very feeble, but on stimulation by contact or other means, the light, passing through a red and green stage, becomes white. Moseley * states that he traced his name on the



FIG. 31 *bis*.—*Pyrosoma elegans*, $\times \frac{1}{2}$ (from Perrier). *a* cloacal opening ; *d* buccal appendages of the zooids.

* *Notes by a Naturalist on the "Challenger,"* London, 1879, p. 574.

surface of a large specimen with his finger, and describes how "in a few seconds his name came out in letters of fire." The

light is emitted by two groups of cells in the region of the mouth. There is a single genus *Pyrosoma* Péron.

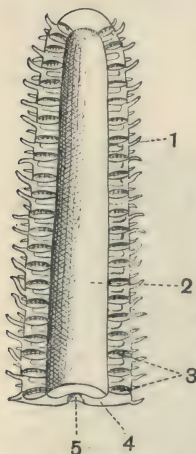


FIG. 32.—Diagram of a section through a *Pyrosoma* colony (after Delage and Hérouard). 1 buccal appendage; 2 common cloaca; 3 zooids; 4 diaphragm; 5 cloacal opening.

The zooids usually lie with their ventral surfaces towards the closed end of the colony, but in *P. elegans* they have the opposite position. There is a buccal and atrial sphincter muscle and a few delicate bands of muscular fibre in the body wall. The test contains cellular elements and some fibrous bands, and the zooids near the common cloacal opening give off two tubular prolongations of the dorsal body-wall containing muscular fibres, which appear to have the function of acting on the diaphragm.

The structure of the zooids is well shown in Fig. 33. The viscera are behind the pharynx, and the anus opens into the posterior part of the atrial cavity. The atrial cavity sends forwards two diverticula, one on each side of the pharynx, but these are not continuous with one another on the dorsal side of the pharynx, as in other Ascidians. The lateral walls of the pharynx consist of from 20 to 50 transverse bars, crossed by from 15 to 30 longitudinal bars. The stigmata are quadrangular, and the longitudinal bars are supposed to be inter-

nal, fine longitudinal bars being absent, as in *Culeolus*, etc., among simple Ascidians and in *Pharyngodictyon* among the Synascidians. It is doubtful however if this interpretation is correct (see p. 12).

There is the usual row of tentacles of which the ventral median is the longest (Fig. 33). The dorsal lamina has the form of 12 languets which show no relation to the transverse bars. The intestine is curved, there is a pyloric gland ramifying on the intestine.

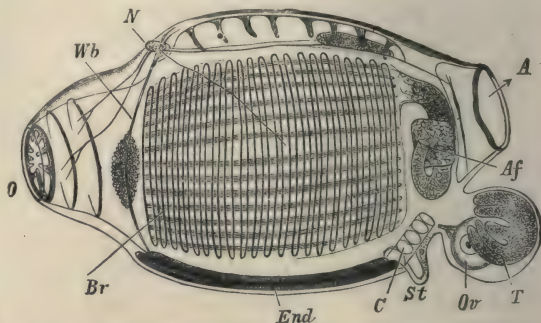


FIG. 33.—A zooid of *Pyrosoma* (from Perrier). A exhalant aperture; Af anus; Br pharynx; Cheart; End endostyle; N nerve ganglion; O mouth; Ov ovary; St stolon; T testis; Wb peripharyngeal ring.

The heart is placed a little behind the end of the endostyle (C). The gonads are placed in the body wall on the ventral side behind the intestine. The ovary contains one ovum which ripens before the testis. The

budding stolon (*st*) is a projection of the ventral body wall and contains a diverticulum of the pharynx which comes off just behind the endostyle, a genital cord, and a prolongation of the pericardium which latter structure is said not to give rise to any organ in the bud. The ganglion carries on its ventral side a pigmented organ which is interpreted as an eye, and the phosphorescent organs (Fig. 33) are paired (right and left) masses of cells containing a fatty substance at the level of the peripharyngeal band in the blood space there found.

The development* of *Pyrosoma* is very remarkable. The ovum is large and full of yolk. The cleavage is partial and gives rise to a disc of cells lying upon the yolk. There is no tailed stage and the development is very different from that of other Ascidians. It takes place within the egg-

follicle and leads to the formation of an imperfect individual called by Huxley the *cyathozoid*. This while still in the maternal tissues produces a stolon (Fig. 34), which immediately undergoes imperfect transverse fission into four parts. Each of these develops into a typical Ascidian zooid, called by Huxley the *ascidiozoid* (Fig. 35). The four ascidiozooids arrange themselves equatorially round the parent cyathozoid (Fig. 35), acquire a common

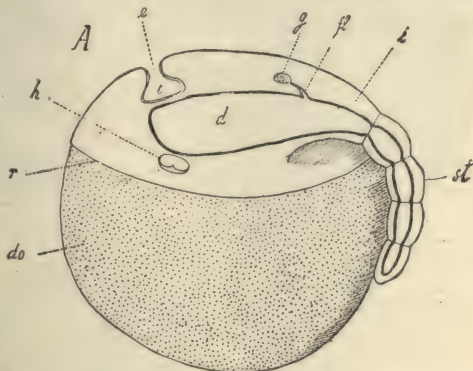


FIG. 34.—Diagram of a *Pyrosoma* embryo showing the developing cyathozoid lying on the yolk with some of its organs developed, and the stolon *st* with commencing fission. *d* enteron; *do* yolk; *e* atrial aperture; *g* ganglion; *h* heart; *fi* ciliated pit, of cyathozoid; *r* edge of germinal disc growing over the yolk of cyathozoid; *st* stolon.

cloaca and form the first individuals of a new colony. The cyathozoid now disappears, the ascidiozooids lose their primary connection, and the little colony passes into the atrium of the parent and thence to the exterior. Each of the zooids composing it possesses a ventral stolon which immediately begins to bud. As all the successively produced zooids have ventral stolons, the colony constantly increases in size and number of individuals until the limit of growth is reached.

Budding by which the adult colony is formed.† Each of the four primary ascidiozooids possesses a stolon at the hind end of its endostyle. This stolon is the pedicle which in an earlier stage connected the zooid to that next it in the chain, *i.e.* it is a part of the original stolon which does not develop into an ascidiozoid. It contains (Fig. 36) a diverticulum of the pharynx (*d*), two lateral bands of mesoderm, an unpaired cord of mesoderm called the genital cord (*g*) and the elaeoblast. Of these structures the mesodermal bands break up and are said not to give rise to organs, while the cord of genital mesoderm which is at first

* Kowalevsky, *Arch. f. Mik. Anat.*, 11, 1875, p. 597.

† Seeliger, *Jen. Zeitsch.*, 23, 1889, p. 595.

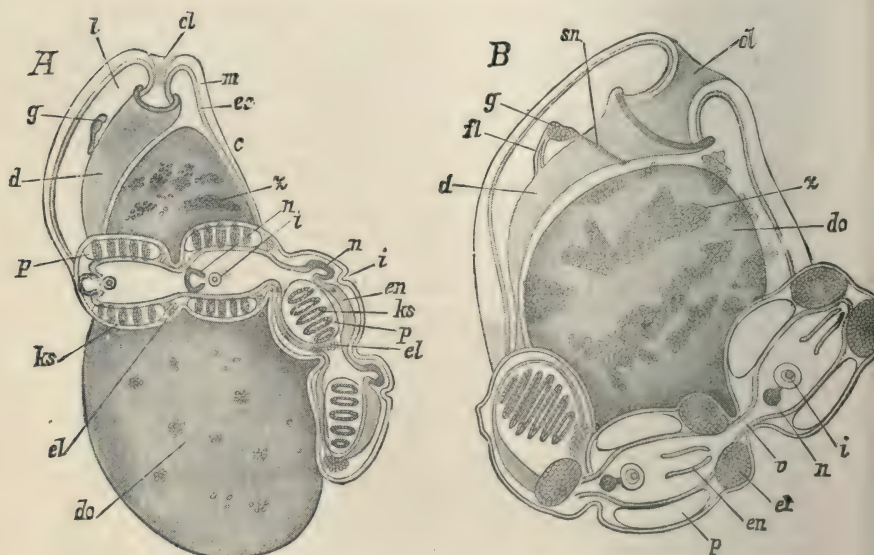


FIG. 35.—Two stages in the development of *Pyrosoma* (after Kowalevsky from Korschelt and Heider). In *A* the yolk of the ovum is partly surrounded by the cyathozoid *c* which has developed on it (see Fig. 34); in *B* the yolk is entirely enclosed by the cyathozoid. *c* cyathozoid, *cl* its atrial pore, *d* its alimentary canal, *do* its yolk; *ec* ectoderm; *el* elaeoblast (a mesoblastic mass in the buds); *en* endostyle of ascidiozoid; *fl* ciliated pit and *g* ganglion of cyathozoid; *i* mouth, *ks* gill-slits of ascidiozoid; *l* vascular space of cyathozoid; *m* test; *n* ganglion of ascidiozoid; *p* peribranchial (atrial) cavity of ascidiozoid; *sn* lateral nerve; *v* endodermal canal connecting ascidiozooids; *z* mesoblast cells.

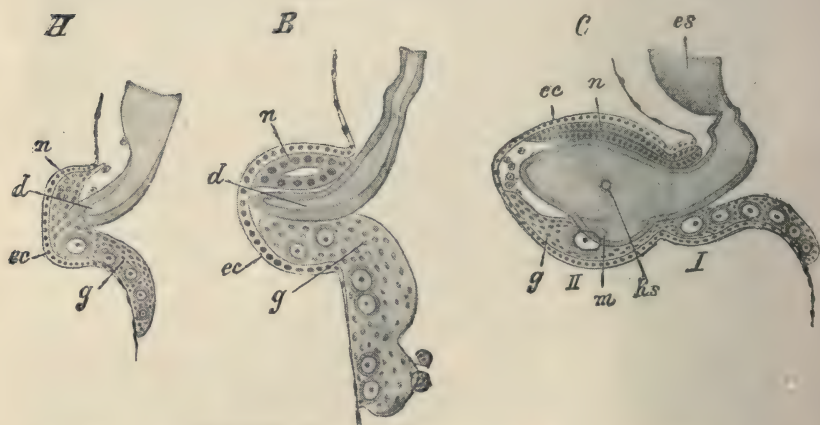


FIG. 36.—Three stages in the development of the proliferating stolon of *Pyrosoma* (from Korschelt and Heider, after Seeliger). In *C* the division of the stolon into two buds, I and II, is indicated. *d* pharyngeal process (epicardium); *ec* ectoderm; *es* endostyle of parent; *g* genital (mesoderm) band; *ks* first gill-slits; *m* rudiment of digestive canal; *n* rudiment of neural tube.

continuous with the rudiment of the genital organs of the parent, gives rise to the peribranchial (atrial) cavity, to the central nervous system (*n*), to the gonads, and to the mesodermal structures of the budding zooid. The pharyngeal diverticulum becomes the pharynx and develops the intestine as an outgrowth (Fig. 37). It is clearly homologous with the epicardium found in many synascidians. The pericardium is developed as a vesicle formed of mesodermal tissue on the right side. It comes to lie on the dorsal side of the pharyngeal process which projects into the stolon of the fully formed zooid (Fig. 37 *pc*), and thus differs in

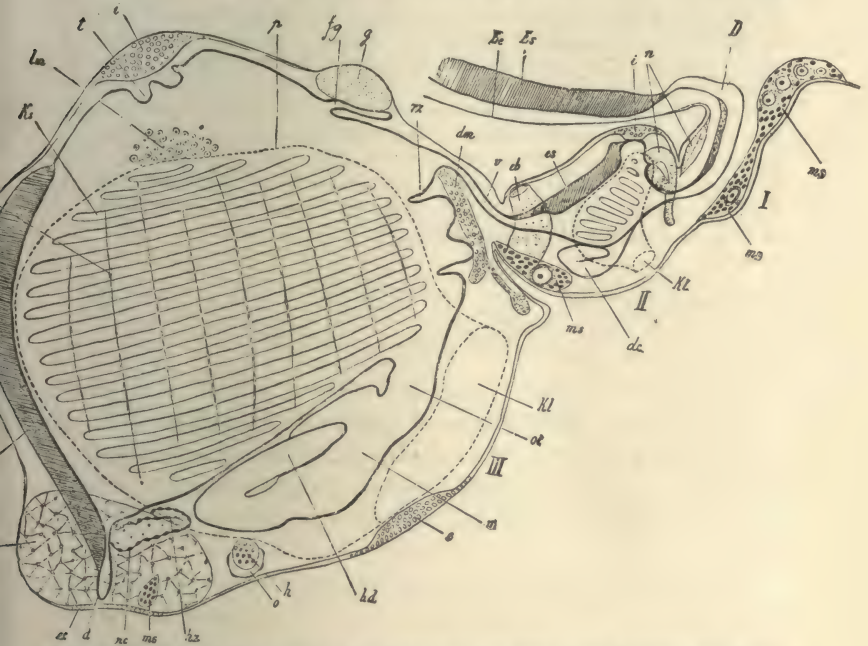


FIG. 37.—A chain of three zooids in the budding of *Pyrosoma* (from Korschelt and Heider after Seeliger), I youngest, II middle and III oldest bud (nearly developed). *D* point at which the pharyngeal process of the parent enters; *d* pharyngeal process (epicardium); *dc* rudiment of digestive canal; *dm* elongated cell mass (? phosphorescent and haematopoietic organs); *e* rudiment of atrial aperture; *eb* elaeoblast; *Ee* ectoderm of parent; *oe* ectoderm of new stolon; *Es* endostyle of parent; *es* endostyle of bud; *fg* ciliated pit; *g* ganglion; *h* testis; *hd* intestine; *hz* heart; *i* rudiment of mouth; *kl* atrium; *ks* gill-clefts; *lf* internal longitudinal gill bars; *lm* phosphorescent organ; *m* stomach; *ms* genital strand; *n* rudiment of nervous system; *o* ovary (egg follicle with egg); *oe* oesophagus; *p* dotted line indicating the boundary of the atrial cavity (peribranchial sac); *pc* pericardium; *rz* languets; *t* tentacle rudiment; *v* tube connecting the enteron of the first and second buds.

position from the pericardium of other forms, which is placed ventral to the epicardium (see p. 15). The nervous system develops from the distal end of the genital cord (Fig. 36) which passes round the front end of the pharyngeal process on to the dorsal surface of the bud and becomes hollowed out to form a vesicle. The ganglion arises from the thickened dorsal wall of this vesicle, the cavity of which acquires a tubular communication with the pharynx and forms the subneural gland and duct (Fig. 37, *fg*). The elaeoblast also develops from the mesoderm, as paired masses which

join round the pharyngeal process (Fig. 37, *eb*). The test of the primary tetrazooid colony is said to be formed entirely by the cyathozooid, but in the subsequent budding each new zooid plays its part in adding to it.

The stolon undergoes fission by transverse constrictions into buds. First one bud is marked off (Fig. 36 *A*), then another between the first and the parent (Fig. 36 *C*), and so on until five have been formed, the youngest bud being always next the parent. When five zooids have thus been marked off, the distal one has acquired full development and becomes detached and a new constriction is formed at the base of the stolon. The new zooids when detached pass round and take up their position near the common cloacal opening of the colony, where the youngest zooids lie. As they increase in age they become further and further removed from this opening by the interposition of the continually forming new zooids.

The points in the above account which must be received with caution are those relating to the origin of the nervous system and peribranchial tubes. In the stolon of the cyathozooid these organs arise as ectoderm invaginations; in the stolons of the later zooids which are directly derived from that of the cyathozooid, they are said to arise from mesoderm. It is difficult to believe that this difference really exists.

Order 2. THALIACEA.*

Free-swimming solitary pelagic forms, which in the adult are never provided with a tail or a notochord. Metagenesis always occurs, and the sexual forms typically remain for some time connected to a process of the body of the asexual form by which they are budded. The mouth and atrial apertures are at opposite ends of the body.

The test is permanent and transparent, and closely adherent to the body. The musculature of the mantle is in the form of

* Traustedt, *Spolia atlantica*, Bidrag til Kundskab om Salperne, *Danske Vid. Selsk. Skrift.*, 1885, p. 339. Kowalevsky and Barrois, *Matériaux pour servir à l'histoire de l'Anchinia*, *Journ. de l'Anat. Phys.*, 19, 1883. Uljanin, *Die Arten der Gattung Doliolum im Golfe v. Neapel*, Leipzig, 1884. Barrois, *Sur le cycle génétique et la bourgeonnement de l'Anchinie*, *Journ. de l'Anat. Phys.*, 21, 1885, p. 193. Seeliger, *Die Knospung der Salpen*, *Jen. Zeitsch.*, 19, 1886. Korotneff, *Die Knospung der Anchinia*, *Z.f.w.Z.*, 40, 1884, p. 50. Id., *La Dolchinia mirabilis*, *Naples Mit.*, 10, 1891, p. 187. Id., *Embryologie der Salpa democratica*, *Z.f.w.Z.*, 59, p. 29, 1895. Id., *Tunicatenstudien*, etc., *Naples Mit.*, 11 and 12, 1895-6. Id., *Zur Emb. v. Salpa runcinata-fusiformis*, *Z.f.w.Z.*, 62, 1896. Brooks, *The Genus Salpa*, *Mem. Biol. Lab. Johns Hopkins University*, 2, 1893. Salensky, *A series of papers on the development and budding of Salpa*, *vide*, *Z.f.w.Z.*, 17, 1876, 30, 1878, *Morph. Jahrb.*, 3, 1877, 20, 1893, *Naples Mit.*, 4, 1883, 11, 1895. Heider, *Beiträge zur Embryologie von Salpa fusiformis*, *Abh. Senck. Ges. Frankfurt*, 18, 1895, p. 367. Metcalf, *Follicle cells of Salpa*, *Zool. Anz.*, 20, 1897, and on the eye and subneural gland in Brooks' *Monograph*, *loc. cit.* Id., *Notes on the Morphology of the Tunicata*, *Zool. Jahrb., Anat.*, 13, 1900, p. 495.

more or less complete circular bands, by the contraction of which locomotion is effected. The pharynx has either two large, or many small apertures leading into a single atrial cavity, which opens to the exterior by the atrial aperture. The anus opens into the atrial cavity. Alternation of sexual and asexual generations (metagenesis) occurs in the life-history and may be complicated by polymorphism (*Doliolidae*). They are only occasional visitors to British shores. A few species of *Salpa* and of *Doliolum* have been taken in the seas around the Hebrides. They are divided into two groups, the *Cyclomyaria* and the *Hemimyaria*, which seem to be sufficiently distinct to merit the rank of sub-orders.

Sub-order 1. *Hemimyaria* (Salpida).

Thaliacea in which the pharynx is reduced to its median dorsal and ventral (endostylar) walls, the lateral walls being absent. The asexual form produces chains of sexual individuals, which give rise again to the asexual form. The muscular rings are usually incomplete ventrally and a tailed larva is not developed.

The salps are transparent pelagic organisms, coloured and opaque at one spot—the nucleus, where the digestive organs and heart are placed. The test is soft and gelatinous and the mantle or body-wall closely adheres to its inner surface. The body is somewhat elongated, with the mouth in front and the atrial aperture behind and slightly dorsal. The muscular tissue (Fig. 38) of the body-wall is arranged in hoop-like bands usually six to nine (there may be as many as twenty and as few as four) which are continuous dorsally, but usually not ventrally, except behind where they constitute the atrial sphincter. At the mouth they are modified in a different way, being prolonged forward into the lips. All these muscles are transversely striated. Dorsally some of them frequently join or approach one another. It is by the contractions of these bands with the mouth closed that water is expelled from the atrial cavity, causing the movement of the animal in a forward direction. The mouth is not lobed, but is bounded by mobile upper and lower lips. It leads into the pre-branchial part of the pharynx, which contains but a single tentacle—the so-called **languet**—on its dorsal side (Fig. 40, 11)

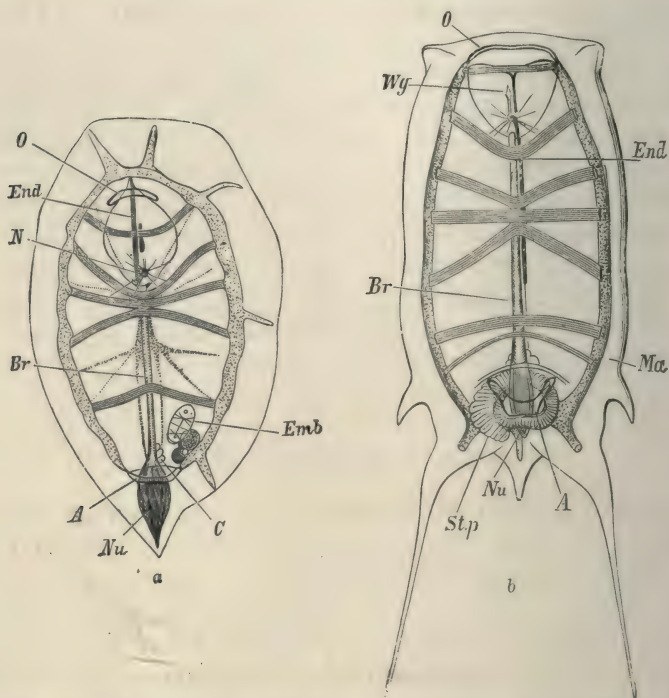


FIG. 38.—a sexual, b asexual form of *Salpa* (*Thalia*) *democratica-mucronata* (from Claus). O mouth; A atrial aperture; N ganglion; Br gill; End endostyle; Wg ciliated pit; Ma mantle; Nu nucleus; C heart; Emb embryo; st.p stolon.

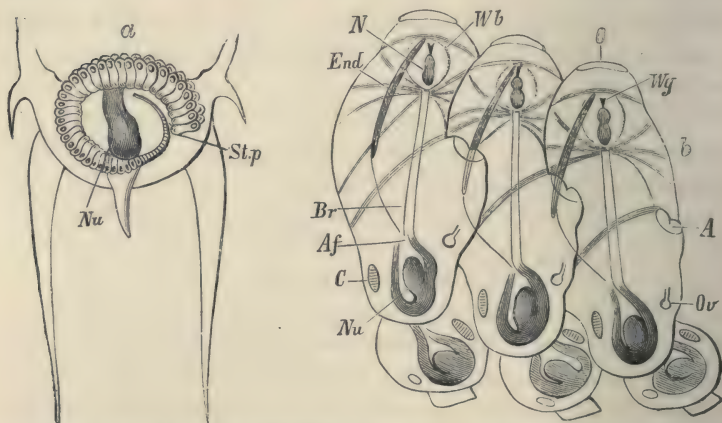


FIG. 39.—a Hind end of *Salpa democratica*, ventral view. St.p stolon; Nu nucleus. b Terminal part of stolon (young chain) magnified. O mouth; A atrial aperture; N ganglion; Wg ciliated pit; Wb peripharyngeal band; End endostyle; Af anus; Br gill; Nu nucleus; Ov ovary; C heart (from Claus).

Behind this is the peripharyngeal band (16), which is grooved in the usual manner.

The **nervous system** and the organs of sense, in correspondence with the power of free locomotion, present a higher grade of development than in the Ascidiacea. The ganglion (13) with its numerous nerves lies dorsal to the anterior attachment of the "gill" and is of considerable size. It has on its dorsal side a horseshoe-shaped brownish-red pigment band, in which are contained besides the pigment numerous rod-shaped structures, the whole directly resting on and being part of the ganglion. There can be but little doubt that this structure is an **eye**.

The dorsal tubercle (ciliated pit) is a short diverticulum of the pharynx in front of the peripharyngeal band; it is without a

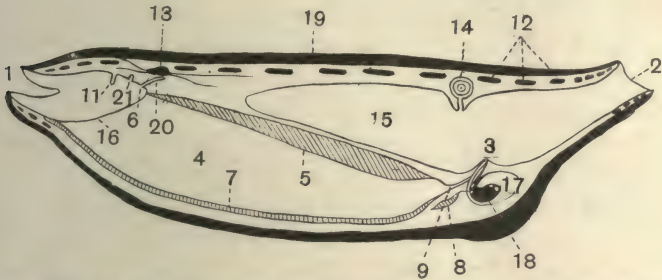


FIG. 40.—*Salpa* in longitudinal vertical section, seen from the left side, diagrammatic. 1 mouth; 2 atrial aperture; 3 anus; 4 pharynx (branchial sac); 5 "gill" (dorsal lamina); 6 duct of subneural gland; 7 endostyle; 8 heart; 9 oesophagus; 11 languet; 12 muscle bands; 13 nerve ganglion; 14 embryo in ovisac; 15 atrial cavity; 16 peripharyngeal ring; 17 stomach; 18 testis; 19 test; 20 subneural gland; 21 dorsal tubercle.

glandular part and does not extend as far back as the ganglion (21). On the ventral side of the ganglion there are two glands (subneural glands) which open by separate orifices into the pharynx (or atrial cavity?) just in front of the peripharyngeal band (6) and behind the representative of the dorsal tubercle. There are no otocysts in salps.

The pharynx is without any side walls or stigmata and freely communicates with the atrial cavity on each side. The endostyle (7) is present in the usual form, and the dorso-median wall of the pharynx is represented by the so-called gill (5) which takes an oblique course across the body from near the ganglion to the opening of the oesophagus where it terminates. The oesophagus (9) leads into a gut which possesses a stomach and pyloric gland,

is twisted on itself and constitutes the **nucleus**. The anus (3) opens into the atrial cavity in the posterior region. In *Cyclosalpa* there is no distinct nucleus ; for the intestine is not twisted but passes forward, along the endostyle in the sexual form, and along the gill in the asexual form, to open anteriorly into the atrial cavity. The **heart** is placed in the nucleus in front of the stomach. In the asexual or solitary form (see below) the pharynx gives off a diverticulum at the hind end of the endostyle which enters the stolon. The **stolon** is a process of the ventral body-wall anterior to the nucleus. It lies in an excavation of the test and contains in addition to this pharyngeal diverticulum a number of other structures which will be described below. Its function is to segment into a number of zooids, which develop sexual organs and differ, when fully formed, in certain features from the asexual animals which arise from the egg. The sexual forms which originate from the stolon remain adherent by processes of the test, and form chains, from which they break off in sections. They are therefore generally found joined to others, but in some cases they become eventually entirely separate from one another. We thus get in the salps the regular alternation of a sexual and an asexual generation. The asexual form is solitary, the sexual usually joined to others in chains. As these two forms differ slightly in anatomical structure and have often been described before their genetic connection was known, they have generally received different specific names. To indicate this connection when it has been discovered and to render the matter perfectly clear, both these specific names are used in the name of the animal ; thus *Thalia democratica mucronata* is a species of which the asexual form was originally described as *Salpa democratica* and the sexual or chain-form as *S. mucronata*, their genetic connection being subsequently discovered. The alternation of generation in salps was discovered at the beginning of last century by the poet Chamisso,* and subsequently rediscovered by Steenstrup.

The sexual form, often called chain-form, *proles gregaria*, or blastozoite,† differs from the asexual form, often called solitary,

* *De animalibus quibusdam e classe Vermium*, Berlin, 1819.

† The terms blastozoite and oozoite are used in different senses by different authors, e.g. the blastozoite is applied to the sexual form because it is produced by budding and to the asexual form because it buds. It is best therefore to discard these terms.

much more elaborate, consisting of eight pigmented structures on the dorsal side of the ganglion.

The development takes place within the follicle described above and is remarkable for the fact that the follicle cells play an important part in transferring nourishment from the maternal organism to the embryo. They do this in two ways: (1) the follicle cells, on the side of the embryo which future development shows to be ventral, proliferate and form a thick mass which soon assumes a cavernous structure. This is the *placenta* (Fig. 43). Maternal blood passes through its spaces and it is continually detaching small masses which, charged with nutritive matter, pass into the vascular system of the embryo and afford nourishment for the growing tissues. (2) The follicle-cells in other parts of the follicle proliferate and migrate in amongst the blastomeres, with which they become inextricably intermingled, so that it is difficult if not impossible to distinguish between them. These cells are called *calymnocytes* (*gonoblasts*). Their fate is much disputed, but there can be but little doubt that they, like the placental tissues, afford nourishment to the growing embryo.

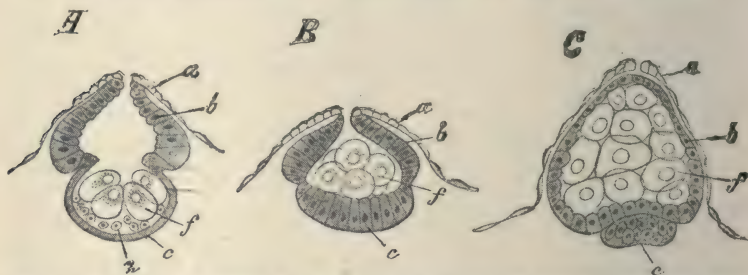


FIG. 42.—Stages in the cleavage of *Salpa democratica-mucronata* (after Salensky from Korschelt and Heider). In A and B the oviduct is open, in C it is closed, and the oviducal and follicular epithelia have combined to form the follicle. a atrial epithelium; b shortened oviduct; c follicle-epithelium; f blastomeres; z calymnocytes. In C, c points to the rudiment of the placenta.

Many views have been held as to the nature of the calymnocytes. Salensky is of opinion that they actually form the embryo, and that the embryo of *Salpa* is a follicular bud and not a true embryo. Brooks thinks that for a time they actually form the embryonic organs but are eventually replaced and probably consumed by the blastomeres.

Meanwhile the embryo has been growing and projecting more and more into the atrial cavity. The follicle cells and the atrial epithelium over it become thin and eventually rupture so that the embryo lies free in the atrial cavity attached only to the placenta (Fig. 43).

The formation of the layers is impossible to follow, but the organs gradually make their appearance in the confused mass of embryonic and follicular cells. With regard to them it is only possible to note a few points here. The **pericardium** is, according to Salensky, developed from the mesoderm; but Korotneff asserts that it arises as a diverticulum of the pharynx, which is perhaps the more usual way in Tunicata. The **ganglion** is by most observers described as arising from a mesodermal mass which becomes secondarily penetrated by an endodermal diverticulum of the pharynx. It is at first hollow and its cavity communicates with the pharynx.

Later it becomes solid and detached from the pharyngeal diverticulum, which persists as the ciliated pit. The two **subneural glands** arise as two invaginations of endoderm further back where the ganglion is in contact with the pharyngeal epithelium. The **elaeoblast** (Fig. 43, *eb*) is a mass of apparently large mesodermal cells in the nucleus in later embryonic life. The large cells of which it consists are filled with nutritive matter, and it is probably to be regarded as reserve of food material. A similar tissue is found in the stolon of *Pyrosoma*. By Salensky it is regarded as a vestige of the tail and notochord of a larval stage.

The **stolon** makes its appearance in the embryo as a diverticulum of the ventral wall of the pharynx between the end of the endostyle and

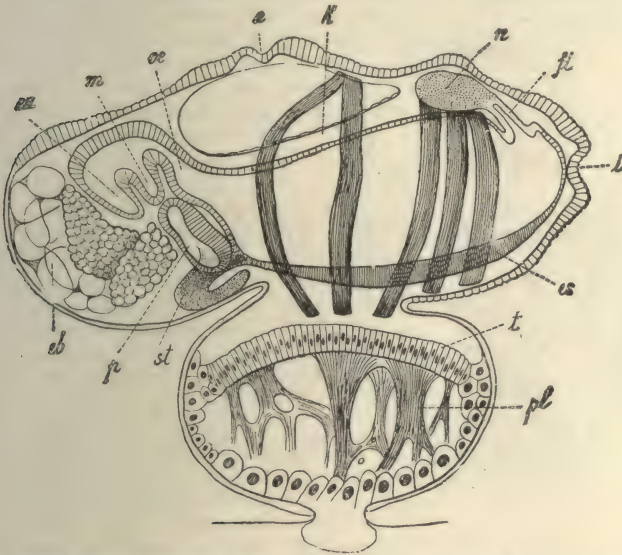


FIG. 43.—Late stage of the embryo of *Salpa democratica-mucronata* (after Salensky from Korschelt and Heider). *a* atrial aperture; *eb* elaeoblast; *ed* intestine; *es* endostyle; *fl* ciliated pit; *i* mouth; *k* gill; *m* stomach caecum; *n* ganglion; *oe* oesophagus; *p* pericardium; *pl* placenta; *st* stolon; *t* basal plate of placenta.

the opening of the oesophagus (Fig. 43, *st*). This soon raises the ectoderm and a small process of the ventral body-wall is formed projecting into the tunic. As this process lengthens a cavity appears between it and the tunic, and acquires an opening to the exterior so that the young stolon lies in a tube formed by the tunic. In some species this tube is directed straight forwards along the ventral side of the body (*Cyclosalpa pinnata*, *Salpa affinis*, etc.). In others it is at first directed forwards, then turns to the left and runs backwards on the left side of the nucleus, opening behind this organ (*Iasis tilesii*, etc.). In yet others (Fig. 39) the tube winds spirally round the nucleus (*Thalia democratica-mucronata*, etc.). With later growth the stolon extends beyond this tube and projects freely uncovered by tunic. Later on the zooids produced on the stolon acquire tunics as a result of their own activity. The projecting part of the chain of zooids is usually

in the form of an elongated band, but in *Cyclosalpa* it has the form of a ring of from seven to twelve zooids attached together. The first rudiment of the stolon contains, in addition to the endodermal tube, a mass of mesoderm derived from the mesoderm of the parent in the neighbourhood of the elaeoblast and possibly from the elaeoblast itself. Stolons a little older contain on the ventral side of the pharyngeal diverticulum a mass of cells called the genital cord, a pair of peribranchial tubes, one on each side of the pharyngeal diverticulum, a pair of mesoderm bands placed immediately outside the peribranchial tubes, a nerve tube on the dorsal side, and a pericardial tube ventral to the pharyngeal diverticulum on the right side.

In addition there are two blood-sinuses, one on the dorsal and the other on the ventral side of the pharyngeal diverticulum; these communicate

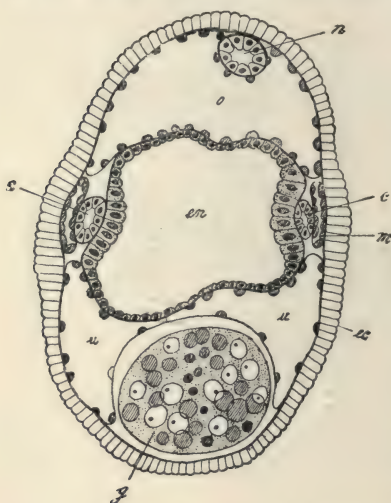


FIG. 44.—Transverse section through a young stolon of *Salpa* (after Brooks, from Korschelt and Heider). *c* peribranchial tubes; *ec* ectoderm; *en* endodermal tube; *g* genital cord; *m* mesoderm band; *n* neural tube; *o* upper, and *u* lower blood-sinus.

with each other at the free end of the stolon and proximally with the blood sinuses in the body of the parent. The neural and peribranchial tubes and mesodermal and genital bands are confined to the stolon and are not continuous with the tissues of the parent. Their origin is doubtful: according to Seeliger they are all differentiations of the mesoderm of the stolon; according to Brooks the peribranchial and neural tubes are derived from the ectoderm of the base of the stolon, while Korotneff maintains that the peribranchial tubes are derived from the endoderm tube. The fate of these structures is as follows: the endodermal tube becomes the pharynx and give rises to the digestive canal, the neural tube yields the ganglion and ciliated pit, the peribranchial tubes the atrial cavity, while the genital

cord gives rise to the genital organs, and the mesoblastic bands to the muscles, pericardium, heart, elaeoblast and mesoderm generally of the future zooids.

In the structure of the stolon and its relation to the parent, and in the formation of the organs, the budding of salps is not unlike that of *Pyrosoma*. The pharyngeal diverticulum clearly corresponds to the epicardial tube. The two processes differ mainly in the much larger number of buds produced by salps before separation from the stolon.

The formation of the buds takes place in the following way. The stolon becomes marked into segments by transverse constrictions due to unfolding of the ectoderm. These are numerous (50 to 100), very close together, and all appear at the same time (Fig. 45). They are the buds which gradually enlarge and develop into the sexual zooids. All the organs of the

stolon are divided by the segmentation except the outer ectoderm, the blood-sinuses, and the endodermal tube. These are continuous from end to end of the stolon, being found in the narrow stalks which connect the buds as well as in the buds themselves (Fig. 45). The stolon has therefore now the form of a chain of developing zooids connected together, the dorsal surface of one to the ventral surface of the next, by short narrow stalks. Meanwhile, the proximal part of the stolon, between the zooids and the parent, has been growing, and undergoing a similar process of segmentation into a group of buds. This process is repeated, so that eventually a chain is formed consisting of groups of from 50 to 100 zooids. The individuals of each group are of the same age, but the groups next the parent consist of younger individuals than the distal and earlier formed groups. As development proceeds a change in the attachment of the zooids is effected. At first they are arranged in a single row, the intermediate constricted part of the stolon passing from the ventral surface of one to the dorsal surface of the next (Fig. 45). Soon, as a result of growth, by which the relations of the parts are changed, and of rotation, they become arranged in a double row, the zooids of one row alternating with those of

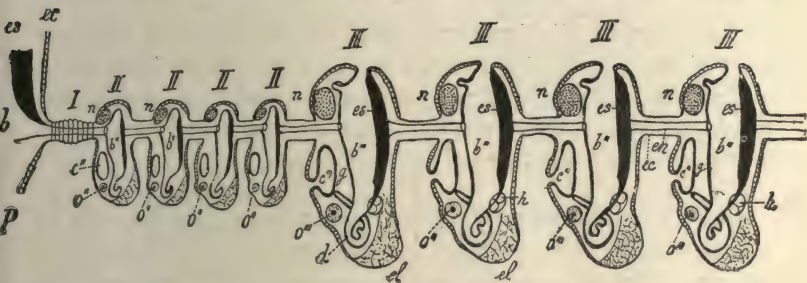


FIG. 45.—Diagram representing a stolon of *Salpa* as it would appear if no secondary shifting of the individuals were to take place (after Brooks, from Korschelt and Heider). *P* solitary form (parent); *I*, *II*, *III*, first, second and third group of individuals (the number shown in each group is much smaller than actually occurs); *b*, *b'*, *b'''* pharynx; *c'*, *c'''* atrium; *d* digestive canal; *ec* ectoderm; *el* elaeoblast; *en* endoderm of the connecting stalks; *es* endostyle; *g* gill; *h* heart; *n* ganglion; *o'*, *o'''* ovary.

the other. Later the intermediate constricted part of the stolon, which joins them, atrophies and the zooids remain adherent by processes of the body-wall and test, which have become developed for the purpose. When this happens the zooids of the group affected become detached from the proximal part of the stolon and form a free-swimming chain of sexual individuals all of the same age and connected by processes of the body wall and test.

The sexual zooids when full grown are of about the same size as the asexual. The ovaries are formed early and the ova are fertilised before the testes are developed. Fertilisation therefore must be effected by spermatozoa produced by another chain.

Cyclosalpa Blainville, digestive tube running antero-posteriorly and not coiled up to form a nucleus; the chain-forms are attached together in a circle. *C. pinnata* Forsk., with linear bands, *C. affinis* Cham., without linear bands. *Salpa* Forskål, digestive tube coiled up in the nucleus, one embryo, chain as elongated band, *S. africana-maxima* Forsk. *Thalia*

Blumenbach, very like *Salpa*, *Th. democratica-mucronata* Forsk. *Pegea* Sav., very like *Salpa* but with supposed traces of stigmata (hemitremata) on its dorsal wall. *Iasis* Sav., like *Salpa*, but with several embryos at different stages of development in the same sexual animal.

The abyssal form *Octacnemus* Moseley, discovered by the *Challenger* Expedition and described by Moseley* is placed here; why, it is difficult to see, for it does not appear to possess any important salp-like feature. *Octacnemus bythius* Moseley, body octoradial, medusa-like, flattened antero-posteriorly, probably attached, test gelatinous, thin, transparent; pharynx with no stigmata or openings into the atrial cavity; digestive organs coiled up to form with the reproductive organs a nucleus which is placed posteriorly; S. Pacific. Our knowledge of its structure is limited, and nothing is known about its budding and reproduction.

A second imperfectly known colonial species† *O. patagoniensis* Metcalfe from 1,000 fms. off the coast of *Patagonia* has been assigned to this genus.

Sub-order 2. Cyclomyaria (Doliolida).

Barrel-shaped Thaliacea with thin test, and pharynx with two rows of stigmata on its posterior wall. The asexual form has a ventral stolon which buds and produces three kinds of zooids, one of which develops sexual organs. The muscular rings are complete ventrally and a tailed larva is always developed.

Doliolum is a transparent pelagic organism with a thin test in which there are no protoplasmic elements and no cellulose. The pharynx (Fig. 46) occupies the anterior part of the body and the atrial cavity the posterior, the digestive canal and the heart (5) together with, in the sexual form, the gonads being aggregated together in an inconspicuous nucleus behind the pharynx on the ventral side of the atrial cavity into which they project. The mouth (1) and atrial (17) openings are at opposite ends of the body and terminal, and the edges of both are lobed. There are no tentacles. The dorsal tubercle (22) is surrounded by the spirally coiled, dorsal ends of the peripharyngeal bands, and the pharynx, which has an endostyle (3) but no dorsal lamina, possesses only two rows of stigmata placed in its posterior wall (20). There is a ganglion and closely adjacent subneural gland (21), which opens in front of the peripharyngeal band by the dorsal tubercle (22). The muscular bands of the body-wall are in the form of complete hoops, of which there are nine in the

* *Trans. Linn. Soc.* (2), 1, p. 287, 1876. See also Herdman *Challenger Reports*, Tunicata, Pt. III, 1888.

† Metcalfe, *Johns Hopkins Univ. Circ.*, 12, 1893, Fig. 8.

asexual and eight in the sexual forms, the anterior and posterior of them acting as sphincters. A tailed larva is formed, and develops into an asexual form which produces a budding stolon. The buds are polymorphic, there being three kinds, one of which alone becomes sexual.

The asexual form (Fig. 46) presents the following features : It has nine muscular rings, and the ganglion is placed behind the fourth. The mouth is surrounded by ten lobes, the atrium by twelve. There is an otocyst (4) in the body-wall on the left side which contains an otolith and in some species opens to the exterior. The body carries two median appendages, a dorsal one (*cadophore*), arising far back near the atrial opening (19), and a ventral one, the stolon (8), arising behind the fifth muscular band. The stolon will be described below. The dorsal process contains a blood space divided into two by a septum, and its dorsal ectoderm is columnar.

In the sexual form (Fig. 47) the mouth is surrounded by twelve lobes, the atrial aperture by ten ; there are eight muscular rings and the ganglion is placed behind the third. There is no otocyst, both the stolon and dorsal appendage are absent, and there is a greater number of stigmata. There is an ovary and a testis, both unpaired ; they open a little to the left of the middle line behind the anus.

The ovary never contains more than one ripe egg at the same time, but as soon as this is expelled a second is formed, and after that a third. After the third egg is laid the ovary atrophies

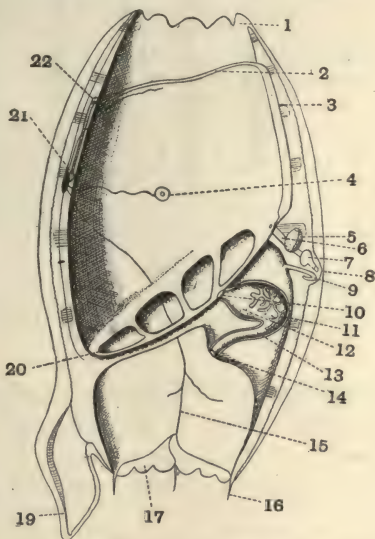


FIG. 46.—Diagram of a longitudinal-vertical section through the asexual (budding) form of *Doliolum* (after Delage and Hérouard). 1 mouth; 2 peripharyngeal band; 3 endostyle; 4 otocyst; 5 heart; 6 left pharyngeal diverticulum; 7 mesoderm; 8 stolon; 9 diverticulum from left side of cloaca into stolon; 10 aperture of oesophagus; 11 pyloric glands; 12 stomach; 13 intestine; 14 anus; 15 nerve; 16 tactile process; 17 exhalant aperture; 19 dorsal appendage; 20 hinder wall of pharynx with stigmata; 21 subneural gland with the closely adjacent ganglion; 22 opening of duct of subneural gland (dorsal tubercle).

and the testis ripens. The egg surrounded by its layer of follicle cells passes into the cloaca and thence into the sea. After

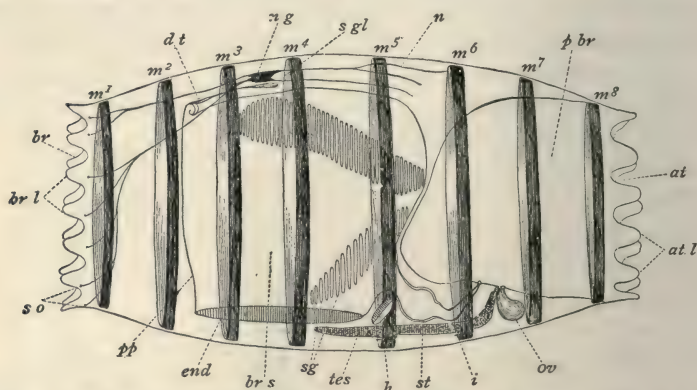


FIG. 47.—*Doliolum denticulatum*, sexual form, from the left side (after Herdman). *at* atrial aperture; *at.l* atrial lobes; *br* mouth; *br.l* buccal lobes; *brs* pharynx; *dt* dorsal tubercle; *end* endostyle; *h* heart; *i* intestine; *m¹* *m⁸* muscular rings; *n* nerve; *ng* ganglion; *ov* ovary; *pbr* atrial cavity; *pp* peripharyngeal band; *sg* stigmata; *sgl* subneural gland; *so* sense organs; *st* stomach; *tes* testis.

fertilisation it secretes a vitelline membrane and falls to the bottom. Here it develops into a tailed larva by a process, of which all the stages have not been followed. It begins to swim by means of its tail while still within the vitelline membrane,

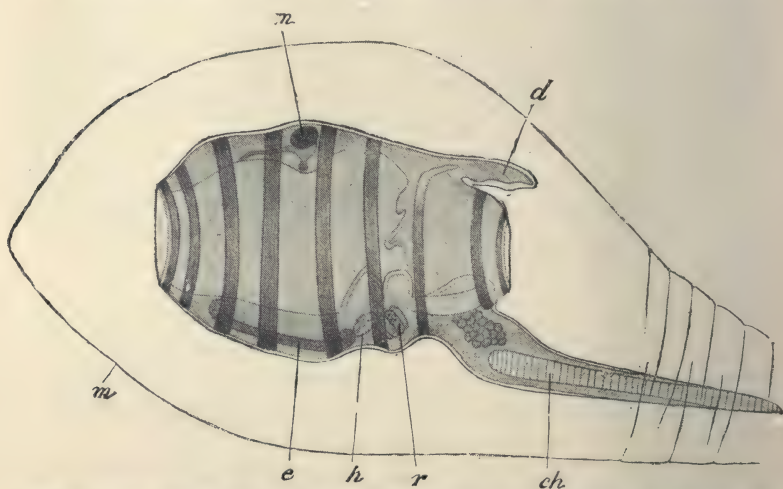


FIG. 48.—Old larva of *Doliolum ehrenbergii* (after Uljanin, from Korschelt and Heider). *ch* notochord; *d* dorsal appendage; *e* endostyle; *h* heart and pericardium; *m* vitelline membrane; *n* ganglion; *r* rudiment of stolon (rosette-shaped organ).

which eventually ruptures and allows the larva to go free. The anterior end of the body assumes the barrel-shaped form of the adult, with its dorsal process, but still preserves its larval tail and notochord (Fig. 48). These eventually atrophy, persisting for a time as a stump, which resembles in structure and position the organ called elaeoblast in the salps and *Pyrosoma*.

The principal features in the development are as follows. Cleavage is total and is followed by an invaginate gastrula. In the next stage observed the embryo appears to contain three cell-groups which constitute the rudiments of the nervous system, the mesoderm and the notochord. The alimentary canal and endoderm are formed later as a secondary invagination of ectoderm. The atrium is formed by another invagination of ectoderm. The nervous rudiment elongates. Its median part remains bulky and gives rise to the ganglion of the adult and the subneural gland (ventral lobe); its anterior end narrows, acquires a lumen which opens into the pharynx, and forms the duct of the subneural gland and the dorsal tubercle; the posterior portion also becomes narrow and persists as the posterior unpaired nerve (*nervus branchialis*). The pericardium is developed as an excavation of a portion of the mesoderm, and the stolon is formed as a small ventral process.

The stolon in its earliest stage in the embryo consists of a small mass of mesoderm applied against the ectoderm in the neighbourhood of the heart.

This is very soon reinforced by two pairs of outgrowths, one from the atrium and the other from the pharynx. These, carrying with them the mesoderm, cause a projection of the ventral body wall, which extends into, but does not pierce, the tunic. Later the stolon pierces the tunic and projects freely, and the five strands contained in it become increased, by development of the cloacal and pharyngeal tubes, to seven. The free end now segments into small bodies (Fig. 50), which become detached and are known as *probuds*. The probuds contain a portion of the seven cell masses surrounded by ectoderm. They wander by means

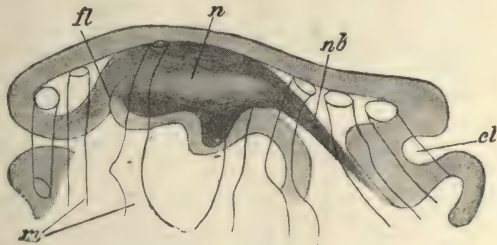


FIG. 49.—Dorsal region of a larva of *Doliolum Mülleri* (after Uljanin, from Korschelt and Heider). *cl* atrium; *fl* dorsal tubercle and duct of subneural gland; *m* muscle-hoops; *n* ganglion; *nb* branchial nerve.

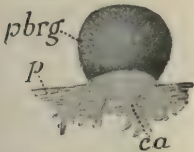


FIG. 50.—Probud of *Doliolum* showing its transporting cells (after Uljanin, from Delage and Hérouard). *ca* transporting cells; *p* wall of body; *pbrg* probud.

of the pseudopodial activity of certain of their ectoderm cells (Fig. 50, *ca*) along the right side of the animal to the dorsal side of the base of the dorsal process (Fig. 51). Here they divide into from fourteen to twenty *buds*, which attach themselves on each side of the middle dorsal line. This

attachment is an epithelial one; they perforate the tunic and their ectoderm becomes adherent to the columnar ectoderm of the dorsal side of the stolon (Fig. 52). By the growth of the stolon in girth they become

displaced outwards and give rise to the *lateral buds* (Fig. 52, *G*) of the dorsal stolon. As the stolon is continually growing in length the buds which first affix themselves are carried away from the body and new buds are attached between them and the base of the stolon. Thus it happens that the buds increase in age as we travel from the body along the stolon.

The probuds which arrive first at the dorsal process give rise to lateral buds (*G*). Those which arrive later give rise to *median buds*, which are attached nearer the middle line and are not displaced so far outwards (Fig. 52, *P*). The fate of the lateral and median buds is as follows. The lateral buds develop into small doliolum-like zooids with the rudiments of gonads, which however soon atrophy, and with a well-developed alimentary canal, but without a closed atrial cavity (Fig. 52, *G*). They actively take in nourishment, and serve for the nutrition of the growing stolon. They are therefore called *gastrozooids*. They are in osmotic relation, through their epithelial attachment to the dorsal stolon, with the blood of the parent. This relation is of some importance, because the asexual parent (*oozoite*) has lost its pharynx and digestive canal by atrophy and, retaining only its nervous system, heart, and muscles, has become converted into

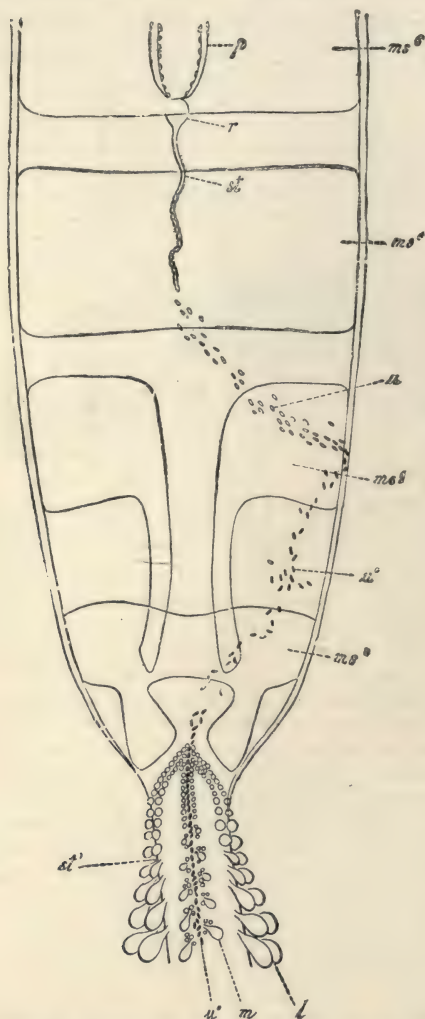


FIG. 51.—Dorsal view of the posterior part of an asexual form (nurse) of *Doliolum* showing the migration of the probuds (after Barrois, from Korschelt and Heider). *l* lateral buds; *m* median buds; *ms* 5-8 four posterior muscle hoops; *p* pericardium; *r* rosette-shaped organ; *st* ventral stolon; *st'* dorsal process; *u* probuds wandering on the ventral side of the nurse; *u'* probuds on the dorsal side, wandering to the dorsal process; *u''* probuds on the dorsal process.

a mere swimming organ (Fig. 53), which propels itself through the sea, by expulsion of water from its atrial aperture like a salp, and draws after itself the trailing dorsal stolon with its four rows of developing zooids.

The median buds develop into *phorozooids* (Fig. 52). These are small doliolum-like creatures with long peduncles of attachment, with eight muscular hoops and with the rudiments of sexual organs, which however soon disappear. As soon as they have reached full development they become detached and swim freely in the sea. On detachment each of them possesses on its ventral peduncle a probud which has

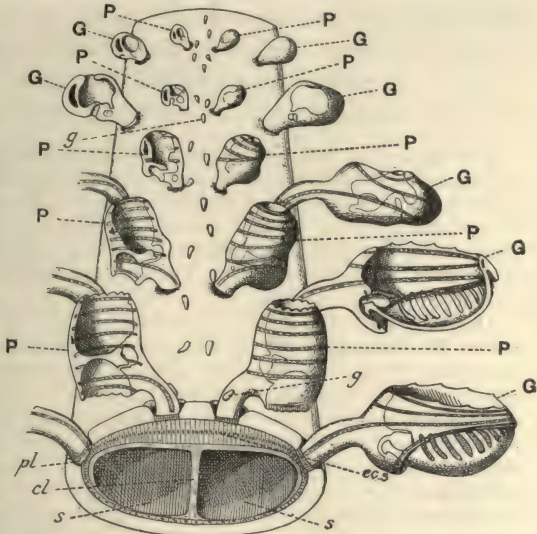


FIG. 52.—Diagram of a dorsal view of the dorsal appendage of *Doliolum* showing gastrozooids *G*, phorozooids *P*, and probuds *g*, destined to give rise to the sexual zooids (after Delage and Hérard). *cl* median septum dividing the vascular space of the dorsal process; *ec.s* thickened dorsal ectoderm of the dorsal process; *G* lateral buds (gastrozooids); *g* probuds which will attach themselves to the peduncles of the phorozooids and form sexual zooids; *P* median buds (phorozooids); *pl* placenta-like connection of ectoderm of bud to ectoderm of dorsal process; *s*, *s* vascular cavity of dorsal appendage. On the left side of the figure the stalks of the three last gastrozooids only are shown. The phorozooids of the left side are shown in longitudinal section, as is the last gastrozooid but one on the right side. The others are shown in external view.



FIG. 53.—Asexual budding form of *Doliolum denticulatum* after atrophy of its alimentary organs, showing the trailing dorsal process with rows of buds. *m* muscles; *ms* median, *ls* lateral buds.

travelled on to it from the dorsal process. This probud divides into from fourteen to twenty buds which attach themselves in the usual way to the peduncle of the phorozooid. Here, during the free-swimming life of the phorozooid, they develop into the sexual form. The sexual form then belongs to the same generation as the gastrozooid and phorozooid. These three forms are all produced by budding from the ventral stolon of the asexual form which arises from the egg.

To sum up the matter, the life-history of *Doliolum* is an example of the alternation of an asexual budding generation which proceeds from the egg and of a polymorphic genera-

tion incapable of budding. The budding form is often called the "nurse"; its buds have three different fates according to the time at which they are produced. The first formed buds become nutritive individuals, called gastrozooids or trophozooids, the next become phorozooids which act as foster-mothers to the latest formed buds, which in their turn become the fully developed sexual animal (gonozooid).

The budding of *Doliolum*, in the early detachment and subsequent fission of the buds, resembles that of the *Distomidae*. The fate of the five cell-masses found in the young probud appears to be as follows. The atrial outgrowths give rise to the nervous system and muscles, the pharyngeal outgrowths to the pharynx, digestive tube, genital organs, and the mesoderm mass to the pericardium. The atrium arises as a dorsal invagination of ectoderm.

Doliolum Quoy and Gaimard, 2 mm. to 3 cm. in length, in most warm seas. The description of the sub-order applies to this genus. There are two other genera, but in neither of them is the budding form known, and our knowledge is in other respects imperfect. *Anchinia* Esch., known only by fragments of the dorsal appendage of the nurse. The buds are arranged without regularity on the dorsal appendage extending on to the ventral surface; the ventral are the oldest. The ventral stolon appears, to lie along the dorsal side of the proximal part of the dorsal appendage. Three kinds of zooids are found upon different fragments of the dorsal appendage, one of which is sexual; the sexual form has 4 muscular hoops and an S-shaped band on each side, 3-8 mm., Mediterranean. *Dolchinia* Korotneff, known only by fragments of its dorsal appendage, on which no remains of the ventral stolon have been found; two kinds of zooids have been found, the phorozooids and the sexual zooids; they closely resemble *Doliolum* and have 8 muscular hoops and a portion of a ninth; both kinds become detached and swim freely, Med., found only once (1891) at Naples, and never since seen, 5 mm.

Order 3. APPENDICULARIAE (PERENNICHORDATA,* LARVACEA, COPELATA).

Pelagic Tunicata of small size, with a persistent notochord and only two gill-apertures. The gill-apertures and anus open directly to the exterior.

* Mertens, Beschreibung der Oikopleura, einer neuen molluskengattung, *Mém. de l'Acad. Petersbourg* (6), 1, 1831, p. 205. J. Müller, Bericht über einige neue Thierformen der Nordsee, *Müller's Arch.*, 1846-7. Huxley, Remarks upon Appendicularia and Doliolum, *Phil. Trans.*, 1851. Id., Further observations on the structure of *Appendicularia flabellum*, *Q.J.M.S.*, 4, 1856. Fol, Etudes sur les Appendiculaires du détroit de Messine, *Mém. de la Société de Phys. et d'Hist. Nat. de Genève*, 21, 1872. Chun, Die pelagische Thierwelt in grösseren Meerestiefen, etc. *Bibliotheca Zoologica*, 1, 1888. Id., Ber. üb. eine nach Canarischen Inseln ausgeführte Reise, *Sitzb. K. preuss. Akad.*, 30, 1889, p. 547. Lohmann, Die Appendicularien der Plankton-Expedition, *Ergebnisse d. Plankton-Expedition d. Humboldt-Stiftung*, 2, 1896. Seeliger, *Bronn's Thierreich*, op. cit.

The *Perennichordata* are free-swimming pelagic organisms provided with a locomotory tail much longer than the body. They usually occupy a cavity, much larger than themselves and opening to the exterior at one or more points, in a gelatinous capsule which corresponds to the test of other *Tunicata* (Fig. 54). They are capable of moving freely in the capsule by the undulations of the tail, and of creating currents of water which flow in and out of the capsule to supply them with food and oxygen. The test or capsule is readily cast off, and the animal then swims freely in the sea, with the hind end of the body forwards. But a new capsule is rapidly formed as a cuticular secretion, not of the whole ectoderm, but of certain parts of it (the so-called oikoplasts). The test contains a few cells, but no cellulose has been detected in it.

The tail, which contains an axial notochord and has two lateral cutaneous expansions, is attached to the ventral side of the body at some distance from its hind end (Fig. 55). The mouth is at the front end, and the anus on the ventral surface anterior to the insertion of the tail, either in the middle

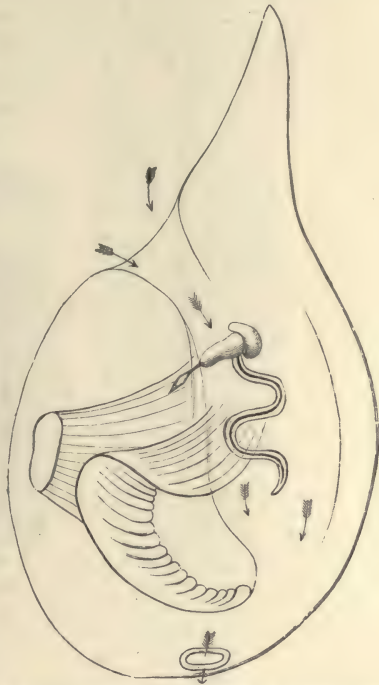


FIG. 54.—*Oikopleura cophocerca* in its test (after Fol, from Seeliger). There are two superior openings, but one only is shown. As the arrows indicate, water passes in by them and out by the lower opening.

line or a little to the right of the middle line. The gill-apertures, often called spiracles, are placed laterally either in front of or behind the anus. The genital organs are in the hinder part of the body behind the insertion of the tail.

The body-wall consists of a simple layer of ectoderm, thickened and glandular in places. There is no dermis, and muscles are usually absent in the region of the body, except in *Megalocercus*.

The whole body is pervaded by a gelatinous substance without nucleated elements (excepting in the tail), but traversed by fibres which run from the ectoderm to the walls of the internal organs,

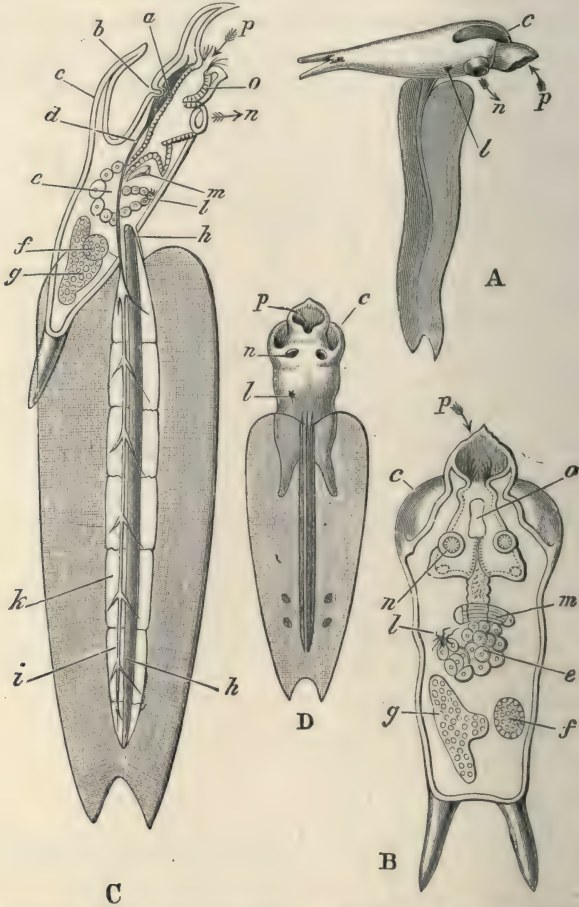


FIG. 55.—*Fritillaria furcata* (after Lankester). A, side view; B, viewed as a transparent object; C, side view as transparency; D, ventral view. *a* otocyst; *b* sensory pit; *c* dorsal hood; *d* nerve cord passing from the ganglion on the right side of the stomach to the tail, where it forms a series of enlargements; *e* stomach; *f* ovary; *g* testis; *h* notochord; *i* nerve cord in tail; *k* supposed myomere of tail; *l* anus; *m* heart; *n* gill-aperture; *o* endostyle; *p* mouth.

and hollowed out along certain tracts to form blood spaces. This absence or paucity of mesenchymatous elements is characteristic and recalls a similar condition found in *Balanoglossus* and *Amphioxus*. The blood-channels are without epithelial walls,

and the blood appears to be entirely devoid of cellular elements. The mouth opens into a spacious pharynx (Fig. 55), and leads behind by a short oesophagus into a dilated stomach, from which passes forward an intestine to open on the ventral surface by the anus. The hind end of the intestine may be marked off as a rectum. There is no pyloric gland or liver except in *Stegosoma* and *Megalocercus* in which a gland, identified as liver, opens by a narrow duct into the stomach. The pharynx has, on the anterior part of its ventral wall, a short endostyle (*o*), consisting of a groove bounded by large glandular cells without cilia except at its front end. From the front end of the endostyle there arises on each side a ciliated band which passes backwards and dorsalwards to join its fellow at the oesophageal opening. There is no dorsal lamina and no row of tentacles. From the hind end of the endostyle a ventral band of cilia, corresponding to the ventral groove of other *Tunicata*, passes backwards to the oesophageal opening. In the ventral wall of the pharynx behind the endostyle are the internal openings of the two gill-apertures; these lead into two short ciliated tubes which open on the ventral side of the body by the spiracles (*n*). There is a small ciliated diverticulum of the dorsal wall of the pharynx, placed on the right side of the ganglion and corresponding to the dorsal tubercle of other *Tunicata*.

The **nervous system** consists of a ganglion (Fig. 55) placed on the dorsal side of the anterior wall of the pharynx, and of a dorsal nerve cord (*d*) which passes back from the ganglion on the right side of the stomach to the tail. In the tail, to the hind end of which it extends, the dorsal cord lies on the left side of the notochord and presents a variable number of swellings due to the presence of nerve cells and called caudal ganglia. The number of these caudal ganglia varies from eight to forty. The first of them is usually larger than the others. Nerves are given off by the cerebral ganglion, and by the caudal ganglia. It has been stated that the cerebral ganglion and dorsal cord contain a minute canal, but this is doubtful.

The position of the caudal nerve cord on the left side of the notochord has suggested the view that the tail has undergone rotation through 90° so that its true dorsal surface has come to lie to the left.

An otolithic vesicle (*a*) lies on the left side of the ganglion, so closely in contact with it that at one place the inner wall of the

vesicle appears to be formed by the ganglion. There are no visual organs. The notochord (*h*) is confined to the tail. It consists of an axial hyaline substance of cartilaginous consistency, surrounded by a protoplasmic nucleated membrane. The nuclei project on the inner side into the hyaline axial substance. The musculature of the tail is well developed. It consists of two broad bands of muscular substance, one on each side of the notochord. Each band consists of an outer protoplasmic layer containing the nuclei and an inner layer of striated contractile substance. The nuclei are ten in number in each band, arranged in a row at regular intervals, thus indicating that the muscular bands are composed of ten cells. The limits of these cells cannot be made out in the adult; though it is said that after certain treatment indications of them may be seen as transverse lines through the muscle substance between the nuclei. (Fig. 55, *k*). It has been suggested that these lines represent the limit of segments and that the tail is segmented. This however is very doubtful. There is no correspondence between the caudal ganglia and the supposed muscle segments.

The **pericardium** is a simple epithelial sac placed on the ventral side of the stomach. Its dorsal wall is contractile and slightly invaginated into its cavity. A concave contractile lamella (Fig. 55) bounding a blood sinus, the dorsal wall of which is formed by the stomach, is thus established. This concave contractile membrane constitutes the **heart**. When it contracts it propels the blood from the superjacent blood sinus into the blood channels generally and so acts as the central organ of the circulation. It is said to reverse the direction of its action as in other Tunicates, but this is doubtful.

The wall of the pericardium is a simple protoplasmic membrane containing nuclei. Dorsally it contains in its outer layer striated contractile fibres. It differs from the heart of other Tunicates merely in the small extent to which the dorsal wall of the pericardium is invaginated.

The **gonads** are contained at the posterior end of the body (Fig. 55, *f*, *g*). Excepting *Oikopleura dioica* all members of the group are hermaphrodite, the male organs maturing first. There is a single or double ovary contained between two testes. There is no oviduct. The eggs when ripe dehisce into the vascular cavity from which they escape by dehiscence of the body-wall,

causing the death of the animal. The testes acquire an opening to the exterior at the time of sexual maturity.

Budding does not take place. What little is known of the development* appears to indicate that it does not differ essentially from that of other Ascidians. The first Appendicularian was discovered by Chamisso, who gave it the name *Appendicularia*. For a long time the systematic position of these forms remained obscure. By many zoologists they were regarded as larval Tunicates, but it was Huxley who discovered their spermatozoa and to whom belongs the merit of having first recognized them as members of the tunicate phylum.

Appendicularia Cham., capsule ovoid, stomach unilobed, rectum enormous, testis single. *Oikopleura* Mertens, capsule large, stomach bilobed, mouth with ventral lip (Fig. 54); tail very long. *Vexillaria* J. Müller, special muscles traverse the body and are inserted on to the viscera. *Stegosoma* Chun, capsule unknown, stomach with liver, surface-waters and deep sea to 1,000 fms. *Megalocercus* Chun, the largest of all known genera, length of body 8 mm., total length 30 mm., capsule unknown, with a body-wall musculature similar to that of the Salps; Med., 600–900 fms. *Folia* Lohmann, capsule unknown, tail long, genital mass single; Atl. *Althoffia* Lohmann, warm parts of Atl. *Fritillaria* Q. and G., body elongated, constricted in the middle at the attachment of the tail, a fold of the dorsal integument forming a hood over the head (Fig. 55), testis usually single. *Kowalevskia* Lahille, capsule large with single orifice, and interior marked with projecting ribs; endostyle, peripharyngeal band, pericardium and heart absent; pharynx with 4 longitudinal rows (a dorsal and ventral on each side) of solid, ciliated comb-like processes which act as strainers; Med. and E. Atl.

* Goldschmidt, *Biol. Centralbl.*, 23, 1903, p. 72.

CHAPTER II.

PHYLUM ENTEROPNEUSTA.

Unsegmented Chordata with a tripartite division of the body and coelom, a dorsal preoral lobe, and a notochord-like structure which is confined to the anterior (proboscis) region of the body. Pharyngeal branchial apertures are present in all except Rhabdopleura.

The Enteropneusta are Chordates * which present the following important features. The body is divided into three regions, the proboscis which is a dorsal preoral lobe, the collar, and the trunk. In the anterior part of the trunk paired lateral apertures—the gill-slits—are present putting the alimentary canal in communication with the exterior (except in *Rhabdopleura*). The coelom, in the cases in which its development is known, arises as five diverticula of the embryonic enteron, viz., one unpaired pouch, which extends into the proboscis and is called the proboscis cavity; one pair of pouches which occupy the collar-region and are known as the collar-cavities; and finally a posterior pair which occupies the whole of the trunk region and constitutes the trunk-cavities. The proboscis cavity opens to the exterior by a single or double pore; the collar cavities each by a pore; while the trunk-cavities are devoid of an external opening.

The anterior part of the alimentary canal sends into the base of the proboscis an unpaired diverticulum which has a characteristic structure and has been identified as a notochord. The central nervous system lies in the ectoderm, and there is a special concentration of it in the dorso-median line of the collar. This concentration comes, in the majority of forms, to lie in the wall of a canal which is open at both ends. There is always a

* See vol. 2. ch. i.

system of tubes which are identified as vascular, and in all there is a curious organ in the base of the proboscis which consists partly of the before-mentioned gut diverticulum and partly of vascular and glandular tissue. This organ is called the **central- or proboscis-complex**. A remarkable feature of the phylum and one which it has in common with the Cephalochorda is the absence or small amount of stellate or other connective tissue cells between the coelomic epithelium and the epithelium of the ectoderm and endoderm (p. 91).

The group Enteropneusta was established by Gegenbaur in 1870 and was placed among the Vermes. They have been regarded by some authors as especially related to the Nemertines and by others as possessing leanings towards the Annelids. Metschnikoff * in 1869 pointed out their resemblances to Echinoderms, while Gegenbaur (1874) and Huxley † (1877) were the first to call attention to the Tunicate affinities, Huxley going so far as to include the two in a new group, the Pharyngopneusta. The connexion with the Vertebrata was suggested by Sedgwick ‡ in 1884, and their inclusion in the group Chordata was accomplished by Bateson in 1885.§

The Echinoderm affinities first pointed out by Metschnikoff undoubtedly exist and are dealt with below (p. 99) and in the section dealing with affinities in the general account of Echinoderms. The suggested affinities with *Phoronis* are discussed at the end of this chapter.

The phylum is divided into two orders, the Balanoglossida and the Cephalodiscida. The establishment of these orders has been necessitated by the discovery of the genera *Rhabdopleura* and *Cephalodiscus*, which present all the important Enteropneust features (except the gill apertures in *Rhabdopleura*).

A great variety of names has been proposed for the phylum here called Enteropneusta. We have selected Gegenbaur's term on the grounds of priority and usage. The discovery of *Cephalodiscus* and *Rhabdopleura*, and consequent necessity for the establishment of two orders within the phylum, have induced some authors to restrict the term Enteropneusta to the forms which we have here included under Balanoglossida, and to employ another name, Hemichordata, for the phylum. We object to this terminology for two reasons: in the first place *Cephalodiscus* is as much

* Ueber Tornaria, *Nachr. K. Ges. Wiss. u. Univ. Göttingen*, 1869, p. 287-292, and *Z. f. w. Z.*, 20, 1870, pp. 131-144.

† *Journal Linn. Soc.*, Zool., 12, 1877, p. 199-226.

‡ *Q.J.M.S.*, 24, p. 70.

§ *Q.J.M.S.*, 25 sup., p. 111.

enteropneust as *Balanoglossus* or *Ptychodera* and cannot logically be divorced from the group to which that name is applied. In the second place, Hemichordata is a bad term, because it is not certain that the structure identified as notochord is really such, and because, even if it is a notochord, it cannot fairly be said to be "hemi." It might perhaps be termed "*probosci*," but no one, so far as we know, has suggested this or applied the name *Proboscichordata* to the phylum.

Order 1. BALANOGLOSSIDA.*

Enteropneusta with vermiform, elongated body and many gill-apertures and gonads.

The *Balanoglossida* are bilaterally symmetrical vermiform animals, which live in sand or mud in the sea. They have a soft ciliated skin which has the property of secreting mucus, a muscular contractile body wall, and are often highly coloured.

The body (Fig. 56) is divided into three regions, the proboscis which is the preoral lobe and overhangs the mouth, the collar (*kr*) and the trunk. The mouth is on the ventral surface at the junction of the proboscis and collar. It is a wide opening and leads into a straight alimentary canal which ends at the hind end of the body in the wide, terminal anus. The hind end of the proboscis (Fig. 56) is narrower than the rest and forms the stalk by which it is attached to the collar region. The anterior end of the collar projects forwards as an annular ridge which completely surrounds this stalk and the mouth. It may therefore be said that the mouth is directed forward; its dorsal side being formed by the proboscis stalk, and its ventro-lateral walls by the ventro-lateral portions of the free upstanding edge of the collar (Fig. 60). The posterior part of the collar likewise projects

* Joh. Müller, Ueb. d. Larven u. d. Metamorphose der Echinodermen, Th. 2., Akad. d. Wissensch. Berlin, 1849, 1850. A. Kowalevski, Anatomie des *Balanoglossus* D. Ch., Mém. de l'Acad. impér. des Sc. St. Pétersbourg, 10, 1866. A. Agassiz, The History of *Balanoglossus* and *Tornaria*, Mem. of the American Acad. of Arts and Sciences, 9, 1873. W. Bateson, A Series of Studies in the Anatomy and Development of *Balanoglossus* in the Q.J.M.S., 24, 25, and 26, 1884-6. J. W. Spengel, Die Enteropneusten, Fauna und Flora des Golfes von Neapel, 18th Monograph, 1893. Id., Die Benennung der Enteropneusten Gattungen, Zool. Jahrb., Syst., 15, 1901, p. 209. Id., Neue Beiträge, etc., ii., iii., iv., Zool. Jahrb., Anat., 20, p. 1, p. 315, p. 413. J. P. Hill, The Enteropneusta of Funafuti, Memoirs Australian Museum, 3, 1898, pp. 205 and 335. A. Willey, Enteropneusta from the S. Pacific, Willey's Zoological Results, pt. 3, 1899, p. 32. R. C. Punnett, The Enteropneusta, Gardiner's Fauna and Geography of the Maldives and Laccadive Archipelagoes, vol. ii. pt. 2, 1903, p. 631. E. W. MacBride, Review of Spengel's Monograph on *Balanoglossus*, Q.J.M.S., 36, 1894, p. 385. S. F. Harmer, Hemichordata, in Cambridge Natural History, vol. 7, 1904, p. 3.

slightly over the anterior end of the trunk, so that there is a circular groove at the junction of the collar and trunk. In some species this hind end of the collar may project so far back as to cover three or four gill-slits (*Dolichoglossus kowalevskii*), and in this case the projection has been called by Bateson the atrial fold, and the space which it encloses the atrial cavity (cf. *Amphioxus*).

The trunk itself is also indistinctly divided into regions: these are the branchiogenital immediately succeeding the collar (Fig. 56, *k*, *g*); next, the hepatic (*vb*), in which the intestinal walls contain a green or brown pigment; and lastly the abdominal region which forms the hind end of the body.

The branchiogenital region possesses in its anterior part on each side of the dorsal middle line a double row of pores; these are the branchial pores which place the gill-apertures of the alimentary canal in communication with the exterior. The branchial pores are placed in a slight

groove, the *branchial groove*. Posteriorly the branchiogenital region is without branchial apertures. The genital organs are also found in the lateral walls of the body in this region.

The **skin** consists of a layer of ciliated epidermis or ectoderm beneath which is a structureless basement membrane. The epidermis is in most parts a thick layer and appears to consist of very long and narrow cells, extending indeed through the whole thickness (Fig. 57) with interspersed unicellular glands. Moreover the nuclei occur at different levels, thus suggesting at

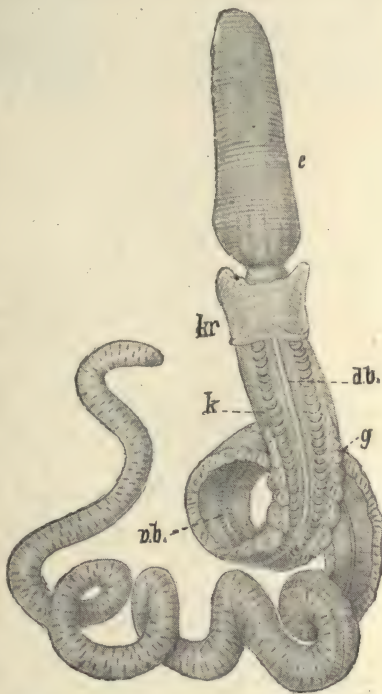


FIG. 56.—*Dolichoglossus kowalevskii* (after A. Agassiz, from Korschelt and Heider). *e* proboscis; *kr* collar; *k* anterior part of branchial region; *g* genital region; *db* dorsal, *vb* ventral middle line.

first sight the view that the epidermis is many-layered. These long cells, into which the epidermis breaks up when teased or otherwise ill-treated, are connected together by numerous lateral processes (Fig. 57), and are prolonged internally into fine fibres which enter the nervous felt-work found in the deeper part of the epidermis over the greater part of the body. The thickness of the epidermis and the number and disposition of the gland cells varies in different places. The muscles and connective tissue are entirely derived from the walls of the

coelomic sacs and will be considered in connexion with those structures.

The nervous system. In the lower stratum of the ectoderm just external to the basement membrane there is the feltwork of fine fibres almost entirely without nuclei, which has just been mentioned. This tissue is supposed to be nervous in function and

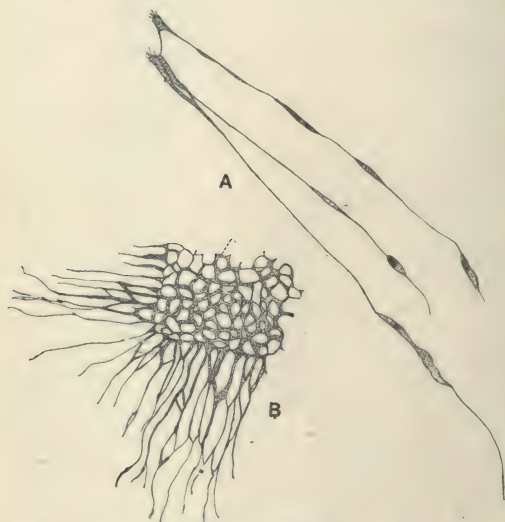


FIG. 57.—Preparations of the epidermis of the collar of *Balanoglossus clavigerus* (after Bateson). *A*, a similar preparation more highly magnified, showing the long spindle-shaped cells passing internally into fine fibres; *B*, portion of epidermis teased and pressed out, showing elongated cells united at their outer ends by numerous connections.

strongly recalls the corresponding layer found in many Nemertini. It is thickened along the dorsal middle line of the collar and trunk and along the ventral middle line of the trunk. These constitute the dorsal and ventral nerve cords (the collar portion of the dorsal cord is invaginated, see below). They are connected at the junction of the collar and trunk by lateral commissures which like them are special concentrations of the nerve plexus and lie in the ectoderm at the base of the collar or atrial groove. The dorsal nerve cord extends forwards on to the base of the proboscis to become continuous with the general

epidermal nerve-plexus of that organ. This is specially developed round the stalk of the proboscis to form the somewhat

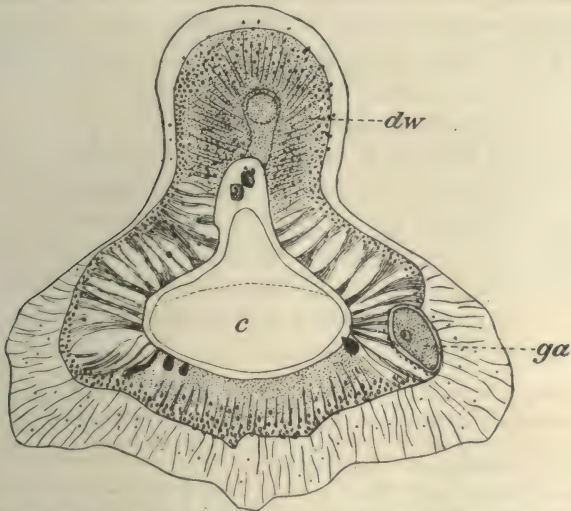


FIG. 58.—Transverse section through the collar nerve cord of *Glossobalanus sarniensis*. showing the central canal *c* with its cuticular lining; *ga* giant ganglion cell, *dw* dorsal root.

ill-defined structure which is frequently spoken of as the proboscis nerve-ring. The part of the dorsal cord contained in the collar has different relations from the rest of the nerve trunks. It

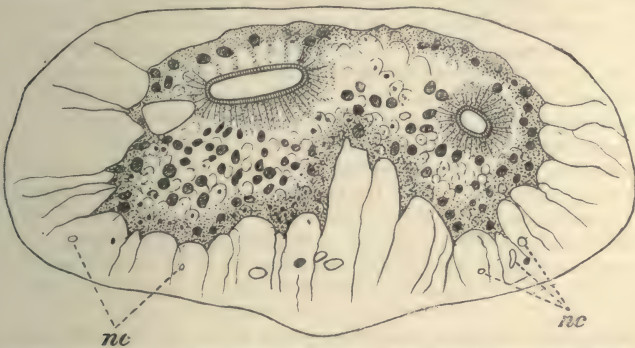


FIG. 59.—Transverse section of the collar nerve cord of *Glossobalanus minutus* (after Spengel). showing two of the isolated cavities with their cuticular lining, and the radiating lines surrounding them; *nc* canals in the fibrous substance which contained processes of the giant cells.

lies in the ventral wall of a tube or rod (Figs. 58, 59, 60) of ectoderm which is derived in the embryo from the delamination

or invagination (according to the species) of a dorsal median tract of collar ectoderm. This collar nerve-cord, which is called the **medullary cord**, is always continuous with the outer ectoderm at the front and hind end of the collar (and in some species by the dorsal roots, see below). At these points (Fig. 60) there is almost always a canal—the **medullary canal**—which in some species is continued through the whole length of the cord. The central canal, whether it is confined to the anterior and posterior ends or extends throughout the whole length of the cord, opens to the exterior by the anterior and posterior nerve pores, the former being placed at the base of the proboscis stalk within the anterior projecting rim of the collar, and the latter at the bottom of the groove (atrial) which is found at the junction of the collar and trunk (Fig. 60).

The fibrous matter of the trunk dorsal nerve-cord is continued along the ventral side of the medullary cord. In the genus *Glossobalanus*, however, the fibrous matter is continued right round the medullary cord, being found on its dorsal surface also (Figs. 58, 59).

In those cases in which the central canal is not present as a continuous tube, it appears to be represented by a number of isolated cavities which are frequently surrounded by elongated radiating cells.* In *Schizocardium peruvianum* and *Dolichoglossus merechkovskyi* the medullary cord is quite solid, there being neither neuropores nor isolated cavities.

There is frequently present at the anterior and posterior ends of the medullary cord an ectodermal pit, with the ectodermal lining of which the nerve cord is continuous. The anterior and posterior neuropores when present open into these pits, or if the cord is entirely solid, as in the two species just named, the medullary cord is continuous with the ectoderm lining them. It is difficult to say whether the pits should be regarded as terminal parts of the central canal or as independent structures. Some importance has been attached to them by Spengel, but as in many cases it is exceedingly difficult to distinguish them from the adjacent parts of the medullary canal, it is perhaps better to regard them as the terminal and, if the central canal is elsewhere obliterated, as persistent portions of this canal. The dorsal nerve cord has the same relation to these pits as it has to the cord, i.e. it lies in their ventral walls. They are sometimes dilated and the anterior pit may project backwards so as to overlap the dorsal side of the adjacent part of the medullary cord (*Spengelia alba*, *Schizocardium*), thus recalling in some degree a cerebral vesicle of the vertebrate brain.

The condition of the central canal varies much even in different species of the same genus. It is present as a complete canal, traversing the whole length of the medullary cord and opening at each end by a neuropore, only in the genus *Ptychodera* (*Pt. flava*, *erythrea*, *bahamensis*), in *Glossobalanus*

* In some cases these isolated cavities are said to coexist with a central canal without however communicating with this latter (e.g. *Sch. brasiliense* in some individuals).

sarniensis, *hedleyi*, *ruficollis*, and in *Balanoglossus apertus*. In other species it is as a rule only present at the anterior and posterior ends, being represented in the middle by a number of cavities (sometimes arranged in a double row [Fig. 59]). In two cases, already mentioned, all traces of the central canal are absent (unless the anterior and posterior pockets are regarded as parts of it), the cord being solid. But even within the limits of the same species it frequently happens that the central canal or its representative exhibits considerable variation.

In the Ptychoderidæ the dorsal side of the medullary cord is connected with the dorsal ectoderm by a variable number of cords which constitute the *dorsal nerve roots* (Figs. 60, 8). These roots are frequently hollow (Fig. 58), particularly those which arise from the anterior end of the cord, and their axial canal communicates with the central canal of the cord or with one of the isolated cavities which represent that structure. The axial canals of the roots do not however open to the exterior, but in some species they may be continued for a short distance in the epidermis as intraepidermal canals (*Balanoglossus carnosus*).

The dorsal nerve roots vary much in number and in the course which they take in reaching the ectoderm. In *Glossobalanus ruficollis* there may be from 12 to 18 of them, in *Ptychodera flava* 1 to 6. As to course, they may be straight or directed obliquely backwards or even curved. In the other families dorsal roots are rarely present. There seems to be a trace of one such structure (not, however, reaching the skin) in *Spengelia porosa*. In *Dolichoglossus kowalevskii* the posterior part of the medullary cord possesses a dorsal keel-like projection, which is solid and does not reach the epidermis. The roots whether solid or hollow consist of cellular prolongations of the cord and are coated with fibrous matter which is a prolongation of that of the cord and is continuous with the nervous stratum of the epidermis.

The ectoderm over the dorsal and ventral nerve cords of the trunk is thickened and sometimes projects as a ridge; in some cases it is partially invaginated and so placed at the bottom of a groove. Moreover it differs from the rest of the epidermis in containing fewer gland cells. As an indication of the fact that the nerve cord of the collar is derived from the completion of such an invagination by the union of the sides of the groove over the gland-free nerve-cord ectoderm, may be mentioned the fact that the ectoderm of the floor of the central canal of the collar cord is more or less free from gland cells, while they abound in the roof. Further, as already mentioned, fibrous nerve matter is usually found only in the ventral wall of the ventral canal. The ectodermal lining of the central canal and isolated medullary cavities possesses a cuticle-like border. It is impossible to arrive at any satisfactory conclusions as to the structure of the nerve tissue. The most that can be said is that the external ends of some of the superjacent ectoderm cells extend into and branch in it. According to Bateson, processes from the fibrous matter of the nerve cords may be traced through the basement membrane into the adjacent muscles.

There do not appear to be any organs of special sense.

The **alimentary canal** extends as a straight tube from mouth to anus. The mouth (p. 68) leads into a wide tube which traverses the collar region and is called the **buccal cavity**. The buccal cavity passes at the junction of collar and trunk into the **pharynx** in the side walls of which the branchial slits are placed; this leads in the hinder part of the branchiogenital region into the **oesophagus** which passes behind into the **intestine**. The anterior part of the intestine is distinguished as the **hepatic intestine** from the posterior part which opens by the anus. The part of the intestine next the anus is distinguished as the rectum. The wall of the hepatic part of the intestine contains a greenish or brown pigment, and in the *Ptychoderidæ* and in *Schizocardium*

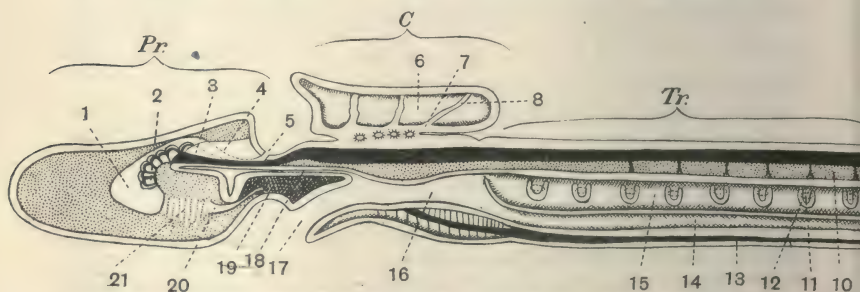


FIG. 60. — Diagrammatic longitudinal-vertical section of *Ptychodera* (from MacBride). *C* collar; *Pr* proboscis; *Tr* trunk. 1 proboscis coelom; 2 glomerulus; 3 heart; 4 pericardium; 5 proboscis pore; 6 collar coelom; 7 collar nerve-cord; 8 dorsal nerve roots of 7; 9 dorsal blood-vessel; 10 dorsal mesentery; 11 external opening of the branchial sac (not clearly shown); 12 U-shaped internal opening of the same; 13 ventral blood-vessel; 14 ventral part (hypobranchial groove) of the branchial region (pharynx) of the alimentary canal; 15 dorsal part of the branchial region of the same; 16 buccal cavity; 17 mouth; 18 notochord; 19 cuticular sheath of the same; 20 ventral pocket of proboscis coelom; 21 ventral mesentery of proboscis coelom.

possesses on each side a row of hepatic diverticula which cause the hepatic sacculations of the body wall visible in these genera. The alimentary canal is lined by a more or less columnar epithelium and is ciliated throughout. It is attached to the body wall in the dorsal and ventral middle lines by longitudinal mesenteries; which however in the adult are deficient in certain parts of the body (see below, pp. 87, 89).

The buccal cavity gives off from the anterior part of its roof, in the dorsal middle line, a forwardly directed cæcal diverticulum (Figs, 60, 64), which, following Bateson, we shall call the **notochord**. The notochord is a tubular structure which extends through the neck of the proboscis and projects into its base. It is divisible into two regions: the narrower neck which lies

in the stalk and opens into the buccal cavity and the wider head which projects into the proboscis-cavity and in which the lumen may be much reduced and not easy to see. At the junction of the two there is a ventrally directed caecal diverticulum (Figs. 60, 64). The walls of this structure are formed of endoderm which is continuous with the epithelium lining the buccal cavity and consists of cells which have undergone a peculiar modification, very similar to that of the notochord cells in *Amphioxus* and in the embryos of the Vertebrata. That is to say, they are much vacuolated and the protoplasm and nucleus occupy but a small portion of them. There is a basement membrane round the whole structure. This, which may be compared to the sheath of the vertebrate notochord, is much developed as a skeletal tissue ventrally and posteriorly (Fig. 60, 19, Fig. 64, n). We shall describe it later on.

There is considerable variability in the structure of the notochord. In transverse section the neck is often semilunar, but its cavity may be broken up into several separate spaces. This is particularly liable to happen in the neighbourhood of the ventral appendage which in some species is very massively developed. In some species portions of the proboscis skeleton may penetrate the substance of the notochord (*Harrimania kupfferi*, *Balanoglossus biminensis*). In *Balanoglossus carnosus* some of the notochordal cells lining parts of its lumen, which are quite cut off from the rest, are densely ciliated. In the same species the hind end of the notochord splits up into three minute tubes which unite again before joining the mouth.

In *Stereobalanus canadensis* the neck is absent, and the head is therefore quite disconnected from the buccal wall. Speaking generally, it may be said that the notochord behind its ventral diverticulum or caecum, quickly loses its chorda-like character. It is interesting to notice that it is in this posterior portion the skeletal development of the sheath is found. May we draw the inference that anteriorly it has a supporting function, while posteriorly this function is taken over by its sheath? In *Schizocardium*, *Glandiceps*, and *Spengelina* the head is continued forwards as a narrow process which traverses the axis of the proboscis and is either solid or contains a small indistinct lumen. This anterior extension is called the **vermiform process** of the notochord. The ventral caecum of the notochord frequently has a considerable lateral extension, whence arise its *lateral pouches* (e.g. *Glossobalanus ruficollis*). The lumen of these structures is often cut off from the main lumen.

The pharynx. The anterior part of the branchiogenital region is occupied by the pharynx, which, as in other Chordata, constitutes the branchial * portion of the alimentary canal. The gill-

* Punnett suggests, as it seems to us with some truth, that the function of the branchial wall with its perforations is more that of a sieve than of a branchial organ, allowing the water which enters by the alimentary

apertures are, except in *Ptychodera* and *Stereobalanus canadensis*, tubes, which lead outward to open externally by the branchial pores placed in the branchial groove on each side of the middle dorsal line. The internal openings (gill-slits) are **U**-shaped, the

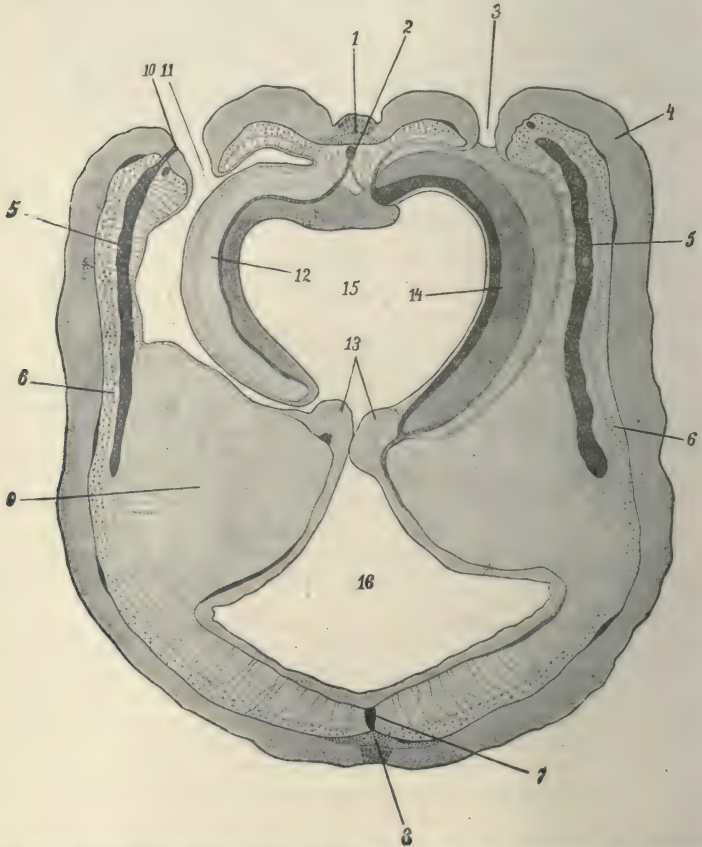


FIG. 61.—*Glossobalanus minutus*, transverse section through the branchial region, somewhat diagrammatic (after Spengel from Lang). 1 dorsal nerve cord; 2 dorsal blood-vessel; 3 branchial (submedian) groove; 4 ectoderm; 5 gonad; 6 longitudinal muscles of body-wall; 7 ventral vessel; 8 ventral nerve cord; 9 trunk coelom; 10 genital pore; 11 branchial pore; 12 tongue bar containing extension of trunk coelom; 13 parabranchial ridges; 14 primary or septal bar, i.e. portion of wall of pharynx intervening between two successive clefts; 15 dorsal part of cavity of pharynx; 16 hypobranchial groove of pharynx, in this region very largely developed.

dorsal margin having a tongue-like projection, forming a tongue-bar (Figs. 60, 62) as in *Amphioxus*. This leads into a pouch

canal with the food to escape. On this view, the skin, which contains a rich plexus of blood vessels, would act as the main organ of respiration.

having the same vertical extent as the gill-slit and placed close to the pharyngeal wall (Fig. 61). This branchial pouch opens to the exterior by a small aperture—the branchial pore. The whole branchial passage is lined by endoderm and is developed as a pharyngeal diverticulum. In the forms just mentioned, the U-shaped gill-slits open directly to the exterior and there are no branchial pouches or pores distinct from them. This is due to the fact that the original pharyngeal outgrowth remains short and its external opening becomes as wide as the internal. The gill-apertures are added to throughout life and arise as small round perforations at the hind end of the pharynx. The tongue is developed as a down-growth of the dorsal wall as in *Amphioxus*, but hangs freely, not as in that animal becoming connected with the ventral margin (Figs. 60, 62). It receives a prolongation of the trunk coelom (p. 92). **Synapticula** (Fig. 62) are present in some species, traversing the two limbs of the U-shaped aperture. They are connected to the tongue bar, and vary considerably in number in the different species; in *Bal. carnosus* there may be as many as 30 on each side of a tongue bar; 10 to 11 seems however to be the usual number. They are absent in the Harmaniidae and in *Glandiceps*. In most forms the gill-slits are not quite straight, being slightly bowed with the concavity directed forward.

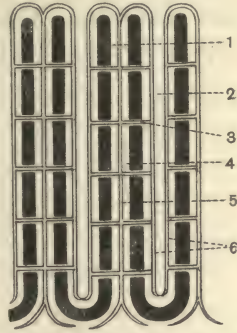


FIG. 62.—Diagram of two gill-slits of *Ptychodera* viewed from the inner side (from MacBride). 1 gill-slit; 2 tongue-bar; 3 synapticulum; 4 septal or primary bar; 5 skeletal rod of primary bar forking ventrally; 6 skeletal rod of tongue-bar, double.

The successive branchial pouches are placed close together, and their opposed walls constitute the *branchial septa*. The first of them always receives the opening of the collar pore (see below), and in *Bal. carnosus* the first branchial pore opens into the hind end of the medullary canal. The gill-apertures are very numerous. The number varies of course with the growth of the animal, and appears to be highly variable in the different species. It varies from 10 or 11 pairs, the number found in *Dolichoglossus sulcatus*, to 700. the number recorded for *Bal. aurantiacus*.

The walls of the pharynx are supported by a definite skeleton recalling the branchial skeleton of *Amphioxus* (see p. 91).

The gill-slits of the two sides are separated from one another dorsally by a narrow streak of endoderm called the *epibranchial streak* (Fig. 63, *A*). Their ventral extension is more variable. In *Schizocardium* they almost meet ventrally, being separated only by a narrow band of endoderm which is called the *hypobranchial streak* (Fig. 63, *C*). In *Dolichoglossus* and *Glandiceps* they extend half way down the pharyngeal wall, being separated by a wide tract of continuous endoderm, which may also be called the hypobranchial streak (Fig. 63, *A* and *B*).

Lastly in the Ptychoderidae and in *Spengelina* they only extend half way down the pharyngeal wall, and the hypobranchial portion is wide as it is in *Dolichoglossus*; but at the junction of

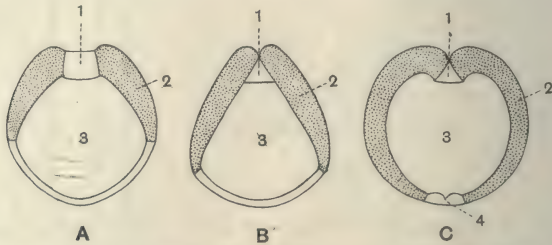


FIG. 63.—Diagrams of transverse section through the pharynx *A* of *Dolichoglossus*, *B* of *Glandiceps*, *C* of *Schizocardium*, showing the vertical extent of the gill-slits. 1 Epibranchial streak; 2 portion of pharyngeal wall perforated by slits; 3 alimentary canal; 4 hypobranchial streak (from MacBride).

the two parts the lining of the pharynx is much thickened, forming the so-called *parabranchial ridges* (Fig. 61, 13) and its lumen is constricted in such a way that the whole pharynx has in section a figure-of-8 shape. The result of this arrangement is that the pharynx is almost divided into two tubes—a dorsal tube in connexion with the gill-slits and a ventral tube comparable to the hypobranchial streak of other forms. In *Glandiceps* two conditions are found; in some species the arrangement resembles that found in *Dolichoglossus*, in others the condition described for *Schizocardium* is repeated.

It seems obvious to compare the epibranchial streak with the hyperpharyngeal groove of *Amphioxus* and the hypobranchial which is so much developed in *Ptychodera* and *Spengelina* with the hypopharyngeal groove or endostyle* of that form. The pharynx sometimes retains its

* The term oesophagus is sometimes applied to the ventral portion of the pharynx, but this is obviously a misnomer and must be rejected.

distinctness for a short distance behind the gill-slits as a groove on the dorsal wall of the oesophagus ; this has been called the *postbranchial canal*.

The pharynx is followed by the **oesophagus** (or afferent intestine as it has been called), which extends throughout the hinder part of the branchiogenital region and leads into the **hepatic intestine**. This structure occupies the anterior part of the abdominal region of the body and is distinguished by the fact that its walls contain green or brown pigment globules. In the Ptychoderidæ and in *Schizocardium* it gives off the hepatic diverticula already referred to. These are arranged in two dorso-lateral rows, one on each side, and open into the intestine by transverse slits. The boundary between the oesophagus and hepatic intestine is not very sharp, especially when the hepatic diverticula are not present.

In *Glandiceps hacksi* there is a kind of **siphonal tube** or accessory intestine in the hepatic region on the dorsal side. It leaves the hepatic intestine at about the middle of its length and joins it again at its hind end.

Spengelina alba is distinguished by possessing hepatic diverticula which do not cause external sacculations of the body wall.

In some species the oesophagus and anterior part of the hepatic intestine sends off dorso-laterally short canals which open to the exterior by pores which are placed on each side of the dorsal surface in a line with the branchial pores. These pores are in two sets. The anterior set comprises the so-called **unpaired intestinal pores**. These are placed in the part of the branchiogenital region immediately following the pharynx, i.e. on the anterior part of the oesophagus, and as their name implies are usually unpaired. They are found in *Schizocardium brasiliense*, 13 on one side and 16 on the other ; in *Glandiceps hacksi* 9 altogether, one on the right side and the rest on the left. The posterior set is known as the **paired intestinal pores**. These are placed at the hind end of the branchiogenital region, or front end of the hepatic, and communicate either with the hind end of the oesophagus or front end of the hepatic intestine. They are found in *Schizocardium brasiliense* (one pair), *Glandiceps hacksi* (three pairs), *Dolichoglossus kowalevskii* (four to six pairs) ; also in *D. mere-schkowskii* and in *Spengelina alba*.

The hepatic intestine passes without any strong line of demarcation into the intestine proper or **efferent intestine** which occupies the hinder part of the abdominal region. This section becomes somewhat narrower behind where it forms the rectum which opens outward by the wide terminal anus.

In most Ptychoderidæ a median rod of endoderm is marked off from the ventral wall of the hinder part of the intestine. It occurs as a thickening of the gut wall, or as a tube with an interrupted lumen opening at both ends into the gut, and has been called the **pygochord**. It lies in what may be called the caudal part of the body and extends back to the anus.

The **coelom**, though largely filled up by muscular and connective tissues in the adult, presents the arrangement which, as we have seen in the first chapter of the second volume (p. 7), is on the whole characteristic of the Chordata (see Fig. 72). It is present in three distinct parts which remain separate from one another: these are the unpaired preoral or proboscideal sac, the paired collar sacs, and the paired trunk sacs. In the embryo these sacs all contain distinct cavities and have epithelial walls (Figs. 72, 73). In the adult the walls have increased in thickness and have become differentiated into the muscular and connective tissues of the body; while the cavities are much reduced, being encroached upon and partly obliterated by these tissues.

The coelom of the proboscis. The wall of the coelomic sac of the proboscis consists of a thin layer of circular muscles lying next the basement membrane of the ectoderm and inside this of a thick layer of longitudinal muscles, which are often arranged in bands and which surround the central cavity (Fig. 65). Within the longitudinal muscles and extending amongst them is a layer of loose stellate connective tissue which partly fills up the proboscis anteriorly.

Into the posterior region of the proboscis cavity there projects a complicated structure known as the **central complex** or the **basal organ** of the proboscis (Figs. 60, 64). The central complex, which consists of the notochord and certain vascular organs, is almost entirely covered towards the proboscis cavity by a layer of coelomic epithelium, and is attached to the body wall in the dorsal and ventral middle lines by the *dorsal* and *ventral* septa of the proboscis (Fig. 65, 1, 6). The posterior part of the proboscis cavity is therefore double and lined, at any rate posteriorly in the region of the dorsal and ventral canals (see below), with coelomic epithelium; while the anterior part (solid in *Harrimania kupferi*) is single (except in *Willeyia* in which it is double) and without, so far as can be seen, a distinct layer of coelomic epithelium. Each of the posterior halves of the proboscis cavity is further subdivided, in consequence of lateral expansions of the notochord which meet the body-wall, into a dorsal and a ventral portion (Fig. 66).^{*} In this way are formed the two *dorsal* and the two *ventral canals* of the proboscis coelom.

^{*} In Fig. 66 the two ventral canals are joined, see below.

The two dorsal canals are lined by coelomic epithelium and extend back into the proboscis stalk (*eh*), where the left of them, and sometimes the right also, opens to the exterior on the dorsal side close to the junction of the stalk with the body, by the proboscis pore or pores. The ventral canals also extend back to the hind end of the proboscis stalk as far as the mouth, where they end blindly (*racemose organ*) or, at most, join one another owing to a deficiency in the ventral septum posteriorly (Fig. 66, *eh v*).

The anterior end of the central complex projects into the proboscis coelom to a variable extent in the different species.

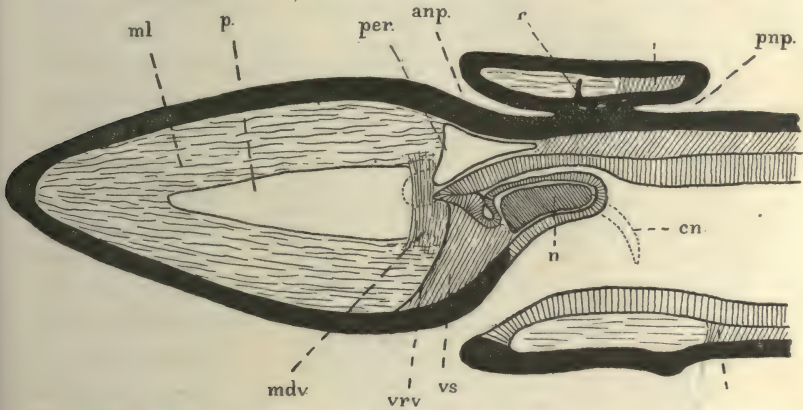


FIG. 64.—Diagrammatic reconstruction of the anterior end of *Spengelia porosa*, $\times 10$ (after Punnett). The dotted line in front of the notochord indicates the forward extension of the pericardial auricles. The heart is omitted. *anp* anterior neuropore; *cn* posterior cornu of nuchal skeleton; *ds* dorsal septum; *mdv* dorso-ventral muscles (muscle-plate); *ml* longitudinal muscles; *n* nuchal or proboscis skeleton; *p* proboscis coelom; *per* pericardium; *pnp* posterior neuropore; *r* dorsal root of medullary nerve cord; *vr* ventral recurrent vessel; *vs* ventral septum.

In some species the notochord is continued forwards in front of the other organs of the central complex for a considerable distance as the vermiform process (p. 75). However far it may extend this anterior extension of the notochord in front of the pericardium (see below) is connected to the dorsal and ventral proboscis wall by a median septum consisting of dorso-ventral muscle fibres which traverse the proboscis cavity and are inserted on to the notochord. These muscle fibres constitute the dorso-ventral muscle plate of Spengel (Fig. 64, *mdv*).* An-

* The transverse sections figured pass behind this muscular septum, excepting possibly dorsally in Fig. 65 (see footnote, p. 83).

teriorly this septum ends with a free edge, the anterior part of the proboscis cavity being single, but posteriorly it overlaps, though it does not join, the dorsal and ventral septa above referred to. In this overlapping part the muscle fibres of the dorso-ventral muscle plate diverge on reaching the central complex and embrace that structure.

The ventral septum consists of a layer of basement membrane which is continuous with the basement membrane of the body wall and with that surrounding the notochord (Fig. 64, *vs*; Fig. 65, 6; Fig. 67, *sv*). It ends with a free edge in front, rarely

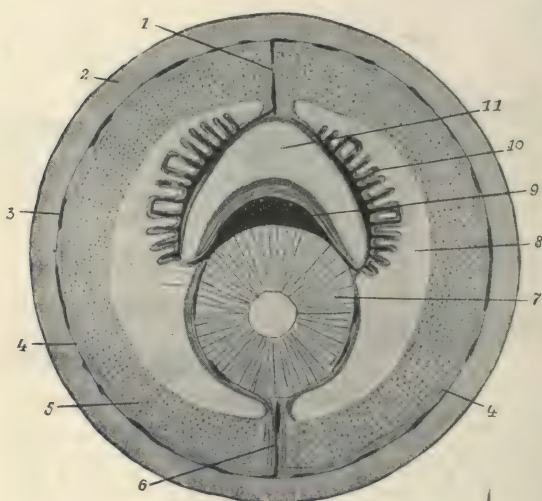


FIG. 65.—Diagram of a transverse section through the proboscis of a *Balanoglossid* (from Lang after Spengel). 1 dorsal septum; 2 ectoderm; 3 blood vessels of the integument; 4 circular; 5 longitudinal muscular layer; 6 ventral septum; 7 notochord; 8 coelom; 9 heart; 10 glomerulus; 11 pericardium.

extending beyond the front end of the central complex, sometimes not so far. Posteriorly it either extends to the very hind end of the ventral canals, completely separating them, or it stops short of this, ending with a free edge, so that the ventral canals join posteriorly (Fig. 66).

The basement membrane of the ventral sep-

tum at the point where it joins the basement membrane of the ventral proboscis wall is pierced by the fibres of the circular muscular layer.

The dorsal septum, which separates the dorsal canals, is formed by the walls of the pericardium, the basement membrane of which is continuous with the basement membrane of the body wall in the dorsal middle line (Fig. 65). It is usually continued forwards as an effective septum by the fibres of the dorso-ventral muscle plate (Fig. 64), which may overlap the anterior portion

of the pericardium,* in the region anterior to the dilated part of the notochord, where the dorsal canals acquire their coelomic epithelial lining.†

The extension of the ventral septum and of the median muscle septum of the proboscis exhibits considerable diversity in the group.

It is now necessary to describe more in detail the posterior more definite portions of the proboscis coelom, where an epithelial lining is present. First of all the ventral canals; they nearly always join posteriorly to form the *ventral cæcum* which extends back to the root of the proboscis (Fig. 66, *ehv*), and the hind end of which in some species forms a small projection (the *racemose organ*) from the roof of the buccal cavity.

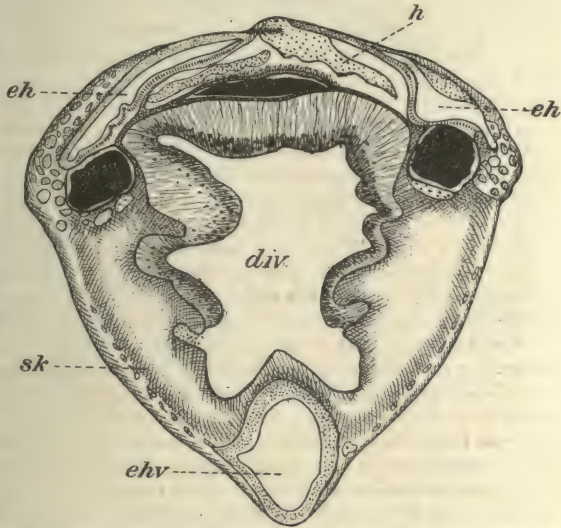


FIG. 66.—Transverse section through the neck of the proboscis of *Balanoglossus gigas* behind the ventral septum (after Spengel). *eh* dorsal canal of coelom, leading on the left side to the pore; *h* tissue in the pericardium; *div* notochord (buccal diverticulum); *sk* proboscis skeleton; *ehv* hind end of ventral canal (ventral cæcum). The efferent vessels of the proboscis are shown on each side dorso-laterally of the notochord.

The dorsal canals are more complicated. They pass backwards in the neck of the proboscis as narrow canals lined with a ciliated epithelium (Fig. 66 *eh*), and they either end blindly or open, at the hind end of the neck, into terminal bladder-like dilatations. These two end-vesicles open to the exterior by the proboscis pores. As a rule there is only one proboscis pore and end-vesicle, viz. on the left side, but when there are two, those of the

* It appears to have done this in the section from which Fig. 65 was taken.

† It will be remembered that anteriorly the proboscis coelom appears to be without epithelium in the adult (see p. 80).

left side are nearly always larger than those of the right. The lining of the hind end of the dorsal canals, whether they end blindly or not, appears to give off nests of cells into the chondroid skeletal tissue (see below), which is found in the neck of the proboscis.

There is the greatest variation in the proboscis pores and in the dorsal canals and in the end vesicles leading to them. In *Ptychodera flava*, *Harri-manina kupferi*, and in *Stereobalanus canadensis* there are almost always two proboscis pores. In *Glossobalanus minutus*, and *Dolichoglossus kowalevskii* there are two in some individuals, but not in all. In *Ptychodera flava* there is the most remarkable individual variation in the arrangement of the dorsal canals leading to the pores. The following variations have been observed: (1) the right dorsal canal ends blindly and is connected by a solid cord of cells with its end vesicle which is smaller than the left and opens outwards by a smaller pore. (2) The right dorsal canal communicates with a wide terminal vesicle by a narrow canal, the lumen of which is occluded; the left canal ends in the chondroid tissue of the proboscis skeleton (see below), in which it gives off numerous islets of cells; the left end-vesicle which is thus not even connected with its canal by a cord of cells, is present and opens to the exterior by the left pore. (3) A similar arrangement to (2) but the right vesicle is in open communication with the right dorsal canal, and there is a solid cord connecting the left dorsal canal and end-vesicle. (4) Both end-vesicles communicate with their corresponding dorsal canals, but the left vesicle is the larger. (5) The right vesicle is larger than the left, and neither of them are in communication with their dorsal canals. Finally, in *Bal. carnosus*, in which only the left pore and vesicle are present, the end vesicle is continued behind the anterior neuropore as two caecal pockets placed ventral to the neural tube, and in some specimens the pore opens into the front end of the medullary tube (for the behaviour of the first branchial pore in this species, see p. 77). When there are two pores the right is said to arise later in development than the left. The lining of the end vesicles is said to be due to an ingrowth of ectoderm; if this is true the actual coelomic pore would be the aperture connecting the vesicle with the dorsal coelomic canal.

The central complex of the proboscis (Figs, 60, 64, 65, 67). Before proceeding to our account of the coelom in the collar, it will be convenient to describe this remarkable structure. It occupies almost the whole of the neck of the proboscis and in the dorsal middle line is in contact with the basement membrane of the ectoderm (Fig. 67). On the ventral side of it is the ventral extension of the proboscis coelom. In some species (*Ptychodera flava* and *erythrea*, etc.) the ventral canal of the coelom extends back as far as the union of the notochord with the buccal epithelium, but in most it stops short of this and the posterior part of the central complex is in contact in the ventral middle

line with the basement membrane of the ventral ectoderm of the proboscis stalk.

The central complex consists of the following parts: (1) ventrally the notochord and, in the stalk, the skeletal developments of the basement membrane of the notochord (Fig. 64, *n*; Fig. 66, *sk*; Fig. 60, *ig*), (2) the heart (Fig. 67, *b*, see also Figs. 60, 65), which is a blood vessel lying on the dorsal side of the notochord, between it and (3) the pericardium (Fig. 64, *per*, Fig. 67, *h*, see also Figs. 60, 65), a closed sac of considerable size and of doubtful meaning, and (4) the glomerulus or proboscis gland which is the well-developed and folded coelomic epithelium lying on the front wall and anterior part of the sides of the pericardium (Fig. 65, *io*, Fig. 60, 2).

The notochord has already been described.

It extends along the whole length of the central complex and varies very considerably

throughout the group. The basement membrane which lies immediately outside its epithelium forms its sheath and is especially thickened on the ventral side of the posterior part of it (Fig. 64, *n*, Fig. 66, *sk*). This specially thickened part of the notochordal sheath is continuous with a specially thickened part of the basement membrane of the dorso-lateral buccal wall (Fig. 64 *cn*), and the whole constitutes the **proboscis** or **nuchal skeleton** (Fig. 68). The proboscis skeleton consists of a median body and of two limbs diverging backwards. The body is placed ventral to the posterior part of the notochord in the neck of the

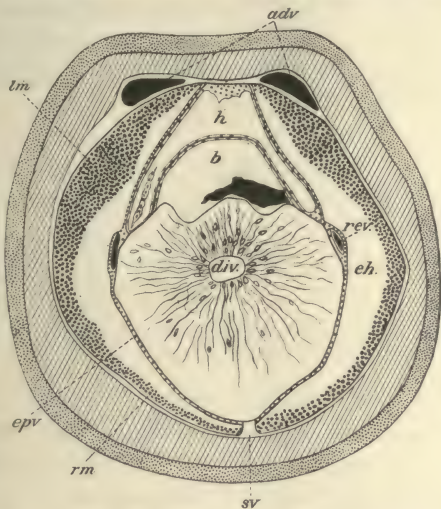


FIG. 67.—Transverse section through the hind end of the proboscis, near the neck, of *Glossobalanus minutus* (after Spengel). The section goes behind the glomerulus. The epidermis is dotted and the nervous layer of the epidermis is diagonally shaded, the basement membrane of the epidermis is unshaded. *adv* blood vessels of skin; *b* heart; *div* notochord; *eh* proboscis coelom divided here into a right and left half by the anterior end of ventral septum *sv*; *epv* coelomic epithelium; *h* pericardium; *lm* longitudinal muscles of proboscis wall; *rev* efferent vessels of proboscis; *rm* circular muscles; *sv* ventral septum.

proboscis. It extends from the hinder side of the notochordal cæcum in front to the junction of the notochord with the mouth behind (Fig. 64, *n*). At this point it divides into the two limbs which diverge backwards into the collar region lying immediately

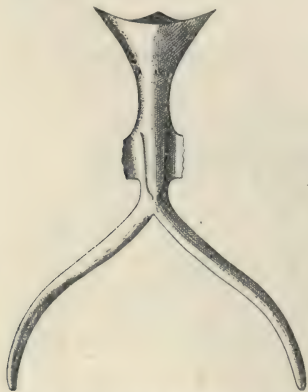


FIG. 68.—Proboscis skeleton of *Glosobalanus sarniensis* (after Spengel).

within the buccal epithelium. The limbs may be long, extending almost through the whole length of the collar, or they may be short reaching but a little way. The proboscis skeleton is strengthened laterally in the hinder part of the neck of the proboscis by the *chondroid tissue*. This tissue is the enlarged basement membrane belonging to the anterior wall of the collar coelom and the posterior part of the dorsal canals of the proboscis coelom. It differs from the rest of the skeletal tissue of the

body in containing nests of cells which have migrated into it from the adjacent coelomic epithelial walls (p. 84). The chondroid tissue, which has a certain resemblance to hyaline cartilage, is specially developed in *Schizocardium* and *Glandiceps*.

The heart is a blood vessel lying in the basement membrane between the notochord and the pericardium (Figs. 65, 67). Its connexions will be described later on when we are dealing with the vascular system. The pericardium or proboscis sac is a closed vesicle lying over the anterior end of the notochord and extending only for a short distance backwards into the stalk (Figs. 64, 65, 67). This posterior part of it is traversed by transversely directed fibres; its anterior part is filled up with a peculiar loose tissue of unknown function while its main body contains a clear fluid. It possesses an epithelial lining which in some cases may proliferate so as almost entirely to fill up its cavity. It has no connexion with the vascular system, and the latest observers have asserted that it is quite closed off from the coelom, but Bateson maintained that its cavity communicates with the coelom through the loose tissue filling up its anterior part. This loose tissue sometimes occupies a large

portion of its cavity (e.g. *Glossobalanus ruficollis*, etc.). Its ventral wall is concave, slightly enveloping the dorsal sides of the notochord, and contains a number of transverse muscular fibres which being in contact with the heart tube very likely cause the pulsations by means of which the blood fluid is moved. In *Schizocardium* (hence the name) and in *Glandiceps* the anterior lateral portions of the pericardium are produced into two tubes which extend along the vermiform process of the notochord and constitute the **auricles** of the pericardium. In *Bal. carnosus* the pericardium is bifid anteriorly, being produced into two pouches, accompanied by glomerulus tissue, beyond the anterior limit of the notochord.

As already stated the dorsal wall of the posterior part of the pericardium is in contact with the basement membrane of the ectoderm, thus giving rise to the dorsal septum; but its anterior wall and the anterior part of its dorsal wall, and its side walls are covered by coelomic epithelium which is much folded and composed of large cells containing pigment grains. This is the glomerulus. Within the folds, i.e. between their epithelium and the pericardial wall are some blood vessels which are in direct communication with the heart. If the glomerulus is an excretory organ, as is supposed by some, its secretion must pass into the proboscis coelom, reaching the exterior by the proboscis pore.

The **collar coelom** is in many species almost entirely filled up by the muscular and connective-tissue development of its walls, and, except in the parts of it known as the collar canals, is devoid of a lining epithelium. The two lateral sacs of which it originally consists meet dorsally above the collar nerve-cord and ventrally below the gut (Fig. 69). The longitudinal mesenteries formed by the opposed walls of these sacs persist only in part: the ventral mesentery is present in the posterior region for a short distance, but is deficient over the greater part of the collar; the dorsal mesentery which extends between the nerve cord and the skin persists over the greater part of its length, but is deficient anteriorly. In *Harrimania kupfferi* both mesenteries are absent in the adult, and it is quite possible that there may be considerable variation in them in other species.

In some genera (*Ptychodera*, *Schizocardium*, *Spengelia* and *Dolichoglossus*), the coelomic sacs of the collar are in parts separated from the gut wall by the *peripharyngeal cavities* (Fig. 69).

which are forward extensions of the trunk coelom and will be described later.

The **collar canals** are two short tubes lined by a ciliated epithelium, and placing the collar-coelom in communication with the exterior. They occur dorso-laterally at the hind end of the collar, and they open externally by the **collar pores** into the first branchial pouch. Internally they open by a funnel-shaped aperture into the collar coelom, which, in the neighbourhood

of the funnel, is free from the tissue elements which pervade it elsewhere. The collar canals are covered towards the coelom by a layer of flat epithelium, and their dorsal walls are often infolded so as to project into the cavity of the canal.*

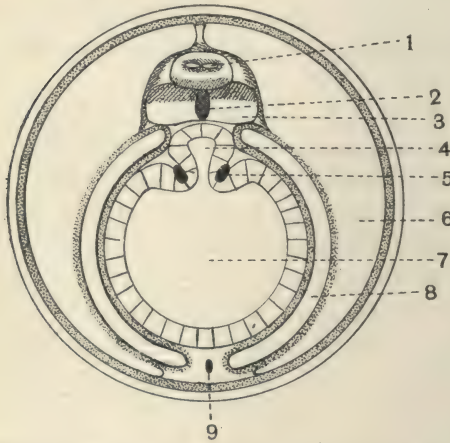


FIG. 69.—Diagram of a transverse section through collar region of a Balanoglossid to show the relations of the body-cavities in the collar (from MacBride). The coelomic spaces are represented as clear of tissue and the ventral mesentery as persistent. 1 medullary nerve cord; 2 dorsal blood vessel; 3 perihæmal cavity; 4 notochord at its point of attachment to the buccal wall; 5 posterior diverging crura of the proboscis skeleton; 6 collar coelom; 7 buccal cavity; 8 peripharyngeal cavity; 9 ventral vessel.

The visceral wall of the collar coelom presents along a certain line on each side a fold containing blood vessels and called the **vascular fold**. In the Ptychoderidæ the vascular fold begins

at the hind end of the collar region and extends along the ventral surface of the alimentary canal in the middle line to a point not far removed from the anterior end of the collar. Here it divides into two folds which pass transversely one on each side to the dorsal surface. In the other genera the fold is double throughout its course. It begins at the hind end of the collar ventrally and ascends obliquely dorsalwards and forwards on each side to the point where the neck of the proboscis joins the body. The vascular folds contain blood vessels which unite the median

* This fold recalls a similar structure projecting into the sand canal of some Echinoderms.

ventral vessel of the trunk with the efferent vessels of the heart. They are obviously to be compared with the glomerulus of the proboscis region.

The **trunk coelom** extends throughout the whole of the body behind the collar. It is a more continuous cavity than that of the collar and is lined throughout by an epithelium and does not open * to the exterior. The dorsal and ventral mesenteries are persistent over the greater part of their course.

The coelom of the trunk, though completely separated from that of the collar, sends forwards diverticula into the collar region. There are two pairs of these extensions. Dorsally on each side of the dorsal blood vessel of the collar, between the collar nerve-cord and the gut, there is a tubular extension of the trunk coelom which extends throughout the whole collar region as far as the insertion of the neck of the proboscis; these are the **perihæmal cavities** (Fig. 69, 3). They are largely occupied by longitudinal muscular tissue which is almost entirely developed from their dorsal walls. The other pair of collar extensions of the trunk coelom constitute the **peripharyngeal cavities** (Fig. 69, 8). These are not present in all genera (see above, p. 87). They lie between the ventral wall of the collar coelom and the gut. In the *Ptychoderidæ* they entirely surround the gut except in the dorsal and middle ventral lines as far forwards as the transversely directed vascular folds described on p. 88. In the other genera in which they are present, they also extend as far forwards as the vascular folds, but these being obliquely directed, they occupy a triangular area on each side of the pharynx.

In the *Ptychoderidæ* the anterior part of the trunk coelom is divided on each side into a dorsal and ventral portion by a septum called the **lateral septum** or accessory mesentery (Fig. 70). The lateral septum passes in the hinder part of its extent from the body-wall, where it is inserted along the submedian line, to the gut wall; while anteriorly it shifts its gut-wall attachment to the body wall near the dorsal mesentery (Fig. 70, B). Moreover, the dorsal section of the coelom gradually dwindles anteriorly and ceases altogether in the branchial region. Posteriorly the lateral septum ends freely and the dorsal cavity opens into the posterior part of the coelom.

* Willey has described structures in *Spengelina*, in relation with the first gill-pouch and the perihæmal cavities, which he regards as vestiges of a pair of coelomic pores for the trunk coelom.

The **muscles** of the collar and trunk are entirely developed from the walls of the coelom. Some of them are developed from the parietal walls and some from the visceral walls both in collar

and trunk, and some from the walls of the collar extensions of the trunk coelom.

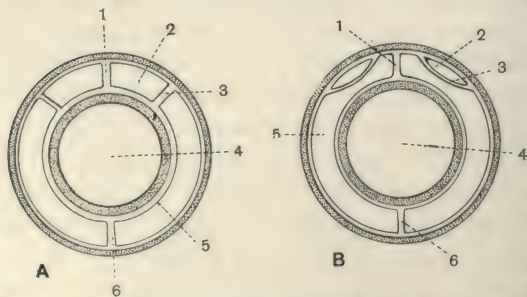


FIG. 70.—Diagrams of transverse sections through the trunk of *Ptychodera* to show the insertions of the lateral mesenteries. *A*, behind the gill region; *B*, through the hinder part of the gill region (from MacBride after Spengel). 1 dorsal mesentery; 2 dorsal division of coelom; 3 lateral septum; 4 alimentary canal; 5 ventral division of coelom; 6 ventral mesentery.

In the case of the collar coelom the whole coelomic wall appears to be converted into either muscular or connective tissue, no portion being left over for lining epithelium save in the collar canals.

The muscles of the body wall of the collar are developments of the parietal wall of the collar coelom. They consist of an external layer of longitudinal fibres and in the anterior region of an inner circular layer as well.

In the trunk the body wall muscles diminish in strength posteriorly. They consist of a layer of longitudinal fibres only, except in the *Ptychoderidae* in which there is an outer layer of circular fibres as well. The layer of longitudinal fibres is interrupted in the dorsal and ventral middle lines and in the submedian lines (where the branchial pores and gonads open).

The visceral muscles of the collar are rather complicated, part of them being derived from the extensions of the trunk coelomic sacs. They are partly longitudinal and partly transverse. Briefly, it may be said that the visceral wall of the collar coelom where it is in contact with the outer wall of the peripharyngeal extensions consists of longitudinal muscular fibres, whereas, where it is in contact with the gut wall, it gives rise to transversely directed fibres. For instance, in *Ptychodera* all the buccal wall behind the vascular fold possesses longitudinal fibres, whereas in front of the vascular fold, transverse fibres only are found. In the other genera the longitudinal fibres are found over the triangular area referred to above (p. 89), while only the transverse fibres are found on the part in front of the vascular folds. The inner wall of the peripharyngeal cavities consists of circular fibres which, together with the partial layer of circular fibres belonging to the visceral wall of the collar coelom, complete the transverse layer of fibres round the gut in the collar region. In addition to the above muscles, radial fibres are found passing across the collar coelom from the visceral to the parietal wall.

In the trunk region the coelomic space is traversed by radial muscular bands and the visceral muscles.

The dorsal walls of the perihæmal cavities give rise to longitudinal muscles which almost entirely fill them. Muscles are also in some genera developed in the ventral walls of these cavities. There are also fibres which traverse the perihæmal cavities.

The muscular fibres seem to be unstriated, but Bateson detected signs of a faint transverse striation in *Dolichoglossus kowalevskii*.

In addition to the muscles above described, muscular fibres are present in the walls of the branchial pouches and in the anterior wall of the collar coelom.

The connective and skeletal tissues and basement membrane.

The Balanoglossida present the remarkable feature of having no connective tissues in the ordinary sense of the word, excepting the delicate reticulate tissue found in the coelomic cavities and extending amongst the muscles. This connective tissue is, as already mentioned, a product of the walls of the embryonic coelomic sacs and appears to be of the nature of mesenchyme. On the other hand all the epithelia of the body possess a kind of internal cuticle, that is to say they secrete on their inner surfaces a continuous structureless membrane devoid of nuclei and fibrous structures. This structureless layer is called the **basement membrane**. It is formed not only on the internal side of the ectoderm cells but also on the inner side of the endoderm and of the walls of the coelomic sacs, even in cases in which these walls have become entirely converted into connective tissue and muscles. It follows from this that not only must there be a layer of basement membrane interposed between all the organs of the body, but also that this interposed membrane must, theoretically at any rate, be in all cases a double membrane, one of its laminae being derived from one and the other from the other of the two organs which are in contact. As a matter of fact this doubleness of the basement membrane is not as a rule discernible, the two laminae of which it is theoretically composed having completely fused. But a separation persists in places and the cavities thus formed constitute the blood vessels (see below).

The skeletal tissues are entirely derived from this membrane. The proboscis skeleton has already been described. Here it is only necessary to call attention to the fact that one part of this skeleton—the chondroid tissue—differs from the rest of the basement membrane of the body in containing strings and nests of nuclei which have migrated into it from the adjacent coelomic walls.

The branchial or pharyngeal skeleton consists of a special

thickening of the basement membrane of the walls of the pharynx on each side the gill-slits. It is made up on each side of a series of structures placed vertically in the walls of the pharynx and presenting a resemblance to a three-pronged fork (Fig. 62). The three prongs of each piece are joined together dorsally and end freely ventrally. The central prong is single (though presenting the appearance when closely examined of being composed of two fused rods) and forks ventrally. It is contained in the septum separating two gill-slits. The anterior and posterior prongs lie in the adjacent tongue bars, which also contain a corresponding prong of an adjacent skeletal piece. The anterior and posterior prongs do not fork ventrally. It would thus appear that each tongue bar contains two skeletal rods belonging to adjacent skeletal pieces. The whole skeleton lies close to the wall of the pharynx. Coelom is present in the tongue bars and its epithelium contributes with that of the adjacent endoderm to the formation of this skeletal basement membrane (Fig. 61). In the primary or septal bars there is no coelom in the adult, so that the skeletal rods in them are exclusively formed by the pharyngeal epithelium.

The **vascular system** consists, as already explained, of channels hollowed out in the basement membranes of the body.

It might be said to represent a persistent portion of the space which theoretically occurs between the two laminæ of which all or nearly all the basement membranes consist. But as the basement membranes do not show a composition of two lamellæ it will be perhaps safer at this point to take the first statement as representing all that we actually *know* on this subject.

The blood is usually described as colourless, but it appears to be coloured red in some forms at least, if we may judge from the fact that a red line can be seen through the body wall along the lines of the chief blood vessels; and it contains a few floating amoeboid cells of the ordinary type.

An epithelial lining is present in the blood vessels of a few forms (*Ptychodera*, etc.), but frequently nothing of the kind can be detected. Some of the larger vessels are provided with muscles (usually circular), which are furnished by the walls of adjacent portions of the coelom. The principal blood vessels are as follows: (1) A longitudinal dorsal vessel running through the body and collar, and passing into the proboscis to become

continuous with the heart. The proboscis portion of this vessel is called the afferent vessel of the proboscis. It runs in the dorsal mesentery, or in what remains of it, in the trunk, while in the collar it is placed between the two perihaemal cavities (Fig. 69). In the proboscis it runs between the notochord and the hind end of the pericardium where it is enlarged to form the heart (Figs. 60, 65). (2) A ventral longitudinal vessel extending through the whole trunk and into the hinder part of the collar (Fig. 69). It runs in the ventral mesentery or in what remains of it. In the collar the ventral vessel divides and becomes continuous with the two plexuses of vessels which are contained in the vascular folds already described. These pass in front into the efferent vessels of the proboscis (Fig. 67 *rev*) which run, one on each side, through the chondroid tissue in the neck of the proboscis to the hind end of the glomerulus, with the blood spaces of which they are continuous. There is in all the basement membranes a capillary network by means of which these main vessels are connected. This network is principally developed in the body wall, in the gut wall, particularly in the hepatic region, and in the gonads. That part of this network which lies in the pharynx wall and is presumably of importance in respiration is of course directly connected with the dorsal vessel. The dorsal vessel is supposed to be contractile and its contractions probably travel forwards, so that the blood passes from it to the heart. From the heart it passes, driven by the contraction of the transverse muscle in the ventral wall of the pericardium, to the spaces within the folds of the glomerulus. Thence it passes into the efferent vessels of the proboscis which are continued from the hind end of the glomerulus through the chondroid tissue into the vessels of the vascular folds and so into the ventral trunk vessel.

There are other main vessels in addition to the two mentioned : e.g., in *Ptychodera* there is on each side in the lateral septa a vessel which arises in the skin in front and enters the intestinal plexus behind ; it supplies the gonads. There are also definite main vessels both in the tongue and primary bars of the pharynx, supplying the capillary network.

The reproductive organs. The sexes are separate and the reproductive organs are similar in form and arrangement in the two sexes. They are simple or branched sacs which project into the coelom and are placed in the lateral part of the trunk in the

branchiogenital region (p. 69). In the simplest cases they form on each side one series, the series of primary gonads, which open to the exterior on the dorsal surface along a line which may be called the *gonaducal* or *sub-median line*. The submedian line lies along the insertion of the lateral septum, where the longitudinal muscular layer is broken, and in the branchial region frequently coincides with the branchial groove, but in *Ptychoderidæ* it is placed at a greater or less interval from the branchial groove and the branchial pores perforate the dorsal longitudinal muscles. In the branchial region the primary genital sacs open externally to the branchial pores (Fig. 61), with which they correspond roughly in number.

The wall of the genital sacs consists internally of a layer of germinal epithelium which is continuous with the ectoderm through the external opening. Outside this is a layer of basement membrane containing an abundant capillary plexus or even a continuous sinus. Then come some muscular fibres and a layer of coelomic epithelium towards the body cavity. It would appear that new gonadal sacs are continually being formed at the hind end of the genital region. In *Ptychodera asymmetrica* gonads are present only on the left side * (Punnett).

The arrangement just described, in which the so-called primary series of gonads alone is present, is the simplest found and is possibly characteristic of all in the young state. It usually becomes more complicated with growth in the following way. The genital sacs become lobed and the lobes acquire independent openings to the exterior (*Schizocardium brasiliense*, *Glandiceps talaboti*). The *secondary pores*, as these are called, are not placed in the line of the primary pores, but are internal or external to them, except in the branchial region, where there are no secondary pores internal to the primary pores. The secondary pores usually open on the submedian line, but some of them may perforate the dorsal longitudinal muscles. A further complication is reached by the complete separation off of some of the lobes, to form a number of *accessory glands* in addition to the original gland which is called the primary gland. These accessory glands are not placed in the series of primary glands but in longitudinal rows—there may be several—either external or internal to the primary row. They acquire their own external openings, which, inasmuch as they belong to the accessory gonads, we shall call *accessory pores*, to distinguish them from the openings of the lobes of the primary glands, which we have called secondary pores. The accessory pores may be either external or internal or both, and they may be placed on the submedian line or perforate the longitudinal muscles.

* Agreeing in this respect with some species of *Amphioxus* (see Goldschmidt on *Amphioxides*, *Wiss. Ergebnisse der "Valdivia" Expedition*, Bd. 12, Lf. 1, 1905, and *Zool. Anzeiger*, 30, 1906, p. 443).

In *Stereobalanus canadensis* there are several rows of gonads, both inside and outside the branchial pores. Their openings are all in the submedian line which is much widened out. In *Ptychodera* there are usually several rows of accessory gonads which are for the most part external to the primary gonads.

The extension of the genital organs varies in the different species. In some species (e.g. *Ptychodera flava*) they are found throughout the branchio-genital region, beginning just behind the collar; in other species (e.g. *Glandiceps abyssicola*) they are confined to that part of the branchio-genital region which lies behind the branchial pores; while in *Stereobalanus canadensis* they are coextensive with the branchial region. In the majority of species, however, they begin in the branchial region at a variable distance behind the collar. In almost all cases the branchio-genital region overlaps the hepatic region, so that genital sacs are found at the anterior part of the latter. In *Bal. carnosus*, however, the transition is abrupt and no genital sacs are found in the hepatic region.

In most of the Ptychoderidæ the side walls of the body in the branchiogenital region are prolonged into winglike folds—the **genital pleuræ**. The genital sacs are for the most part contained in these wing-like outgrowths, but not entirely, for in some species they are found in the body as well, mediad of the insertion of the lateral septum. The genital pleuræ are extremely mobile structures and may be bent up so as to cover the back of the animal. In *Bal. carnosus* their free opposed edges may become united by mucus, so that a cavity, widely open behind and receiving the branchial pores, is formed on the dorsal side of the branchiogenital region.

The gametes are produced from the walls of the gonads and when ripe are passed out to the exterior through the genital pores. The spermatozoa have spherical or oval heads and active flagelliform tails. The ova are provided with a close-fitting egg-membrane, and are of two sizes according to the amount of yolk and manner of development.

In most genera the egg is small, varying from .06 mm. in diameter in *Ptychodera flava* to .15 mm. in *Bal. carnosus*. The development of such eggs is probably indirect, passing through a free larval stage, called the **Tornaria** (Fig. 74). In some cases, however, the eggs are much larger, varying in their longest diameter from .4 mm. in *Dolichoglossus kowalevskii* to 1.5 in *Harrimania kupferi*.

The early stages of the small eggs which probably develop into tornaria are not known, but thanks to the researches of Bateson all the stages of the development of *Dolichoglossus*

kowalevskii are known. The eggs of this species are laid singly and deposited in the muddy sand which the animal inhabits. Segmentation is regular and complete and leads to the formation of a spherical blastosphere which becomes a gastrula by invagination (Fig. 71, A). The blastopore narrows and a circle of cilia is formed round it; it eventually closes up at that pole of the egg which will become, as shown by the persistent ciliary circle, the future hind end; i.e. it closes in the position of the future anus. The embryo becomes covered with fine cilia and a tuft of longer cilia is formed at the anterior end. The

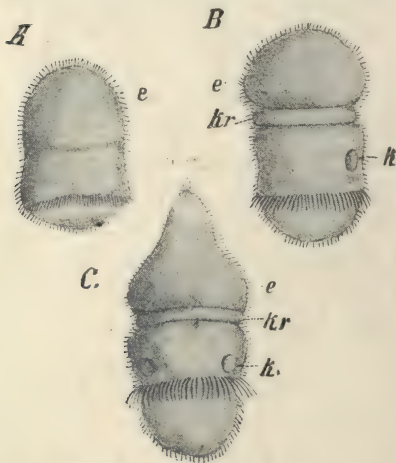


FIG. 71.—Free-swimming larvæ of *Dolichoglossus kowalevskii* in different stages of development (after Bateson, from Korschelt and Heider). . e proboscis; k branchial pore; kr collar.

embryo elongates and two transversely directed grooves appear, marking out the three regions; proboscis, collar, and trunk (Fig. 71, B). The embryo hatches at about this stage and lives as a free larva which at first swims in the mud by means of its cilia, and later burrows in the mud by means of its proboscis (Fig. 71, C). A groove appears in the collar region in the dorsal middle line marking the position of the medullary nerve-cord which is now being developed. This groove is a temporary structure and does not appear to participate in the formation of the collar nerve-cord which arises by delamination from the ectoderm. The first gill-slits now appear just behind the collar as a pair of perforations, and the mouth is formed as a minute perforation in the groove between the collar and proboscis. The anus is formed rather later at the hind end.

Meanwhile the five coelomic pouches have made their appearance; one unpaired pouch in front and two pairs behind (Fig. 72). These become closed from the gut and persist as the coelomic sacs. All the mesodermal tissues are derived from the walls of these sacs.

The collar nerve cord is delaminated from the ectoderm beneath the transient groove already mentioned. It remains however connected with the ectoderm throughout life at its front and hind ends. It appears to increase in length at the front and hind ends of the collar by invagination of the median ectoderm, by which process the continuous central canal present at these points is formed.

In the subsequent changes the gill-slits increase in number from before backwards and the adult form is gradually assumed (Fig. 71, *C*). A larval organ, constituting a suetorial tail for attachment, is developed and lasts for a short time; it is placed at the hind end ventral to the anus. The notochord is formed as a dorso-median groove of the anterior part of the gut which becomes partially constricted off from before backwards to form a tube; it later extends into the base of the proboscis. The pericardium is developed from a solid mass of cells derived from the wall of the posterior part of the proboscis coelom. The first trace of the generative organs is seen when there are 10 gill-slits. Their exact origin was not made out in this species, but from observations of other

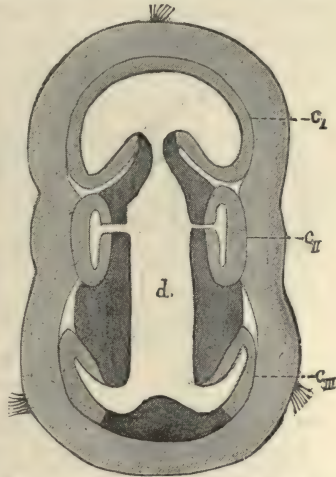


FIG. 72.—Diagram of a longitudinal section through a larva of *Dolichoglossus kowalevskii* (after Bateson, from K. and H.). *c*₁ anterior (proboscis), *c*₁₁ middle (collar), *c*₁₁₁ posterior (trunk) coelomic diverticula, *d* enteron.

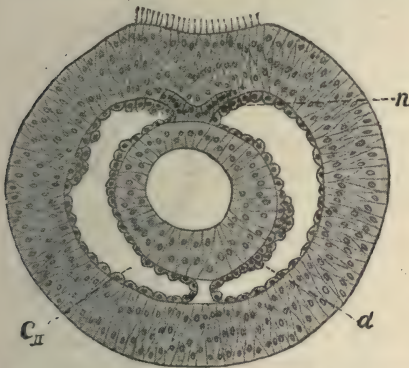


FIG. 73.—Transverse section through the middle part of the collar of a larva of *Dolichoglossus kowalevskii* which is at about the stage of Fig. 71 *B* (after Bateson, from K. and H.). Above is seen the dorsal ciliated groove. *d* enteron; *n* rudiment of nerve cord; *c*₁₁ collar coelom.

an earlier stage (Fig. 72), a proliferation of the coelomic wall occurs in the dorsal middle line; this causes a projection into the cavity which

species they are probably mesodermal, though by some observers they are believed to be derived from the ectoderm, with which in any case they soon become connected. So far they have not been traced into connexion with the coelom.

The proboscis pore is first indicated by a thickening of ectoderm on the base of the proboscis. This thickening acquires a cavity which later opens to the exterior and to the proboscis coelom. The collar pores arise by the perforation of thickened patches of ectoderm in close connexion with the opening of the first gill-slit. At the posterior end of the proboscis coelom, at the point where the coelom was connected with the gut in

eventually reaches the ventral wall. The hinder part of the proboscis coelom thus becomes divided into two parts by a vertical septum. Some of the cells of this septum give rise to the pericardium, which when first formed is solid, and later on the notochord grows into it.

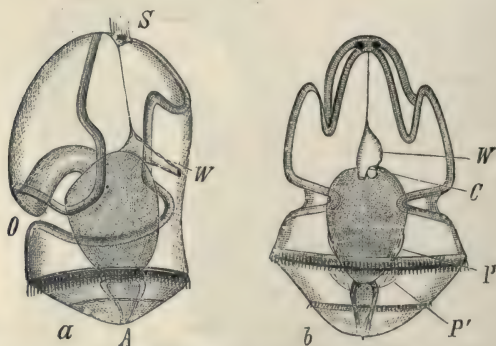


FIG. 74.—*Tornaria* larva (after Metschnikoff), *a* from the side; *b* from the dorsal surface; *A* anus; *C* pericardium; *P, P'* coelomic sacs; *O* mouth; *S* apical plate; *W* rudiment of the proboscis coelom (so-called water-vascular sac).

it for an Echinoderm larva. Its real nature was determined by Metschnikoff. The early stages of this development are not known, but the later stages by which the larva passes into the adult have been more or less worked out. In the youngest stage known, the *tornaria* has a somewhat ovoid form with a ventral mouth, a terminal anus, and an alimentary canal divided into three regions, viz., oesophagus, stomach and intestine (Figs. 74, 75). There are two ciliated bands, one of which is preoral and encircles the preoral lobe, and the other postoral but longitudinal in direction. These two bands touch one another dorsally and anteriorly, the ectoderm at the point of junction being thickened to form the apical plate (*S*). The apical plate possesses nerve fibres and ganglion cells and soon acquires a tuft of immobile cilia. It also contains a pair of pigmented eye spots.

Internally there is a spacious blastocoel, in the front part of which is a vesicle called the water-sac (Fig. 74). This is the

The *tornaria* larva. In most species which have eggs of the smaller size, the development is indirect and a transparent pelagic larva known as the *tornaria* is developed. This larva was first described by J. Müller, who took

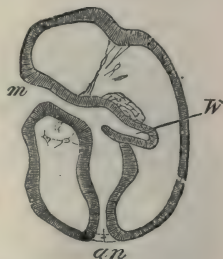


FIG. 75.—Early stage of a *tornaria* larva in longitudinal section (from Balfour after Goette). *m* mouth; *an* anus; *w* rudiment of proboscis coelom (so-called water-vascular vesicle).

rudiment of the proboscis coelom. It lies on the hinder part of the oesophagus and is connected to the apical plate by a muscular band, and opens on the dorsal surface by a short ciliated tube, the rudiment of the proboscis canal and pore of the adult. The pericardium (heart-vesicle), the origin of which is uncertain, lies at first near the skin to the right of the proboscis pore. It soon leaves the surface and becomes surrounded by the proboscis coelom. By some authors it is regarded as the right proboscis cavity. Later a transverse circumanal ciliated ring is formed, and sometimes a second less distinct ring behind this. Moreover the course of the two first described ciliated bands frequently becomes complicated and folded, and in *Tornaria grenacheri* they acquire ciliated lobe-like projections.

In the later development the form of the adult is gradually attained; the ciliated rings disappear and the two posterior pairs of coelomic sacs are developed in a manner which has not been thoroughly ascertained. The collar nerve cord, gill-slits etc., are formed as they are in the direct development.

The tornaria has by its ciliated bands and general form a strong external resemblance to the bipinnaria larva of an echinoderm, a resemblance which is increased by the presence of the so-called water-vesicle with its dorsal pore; and when first discovered it was described as belonging to that group. A close examination of its structure, though revealing points of difference

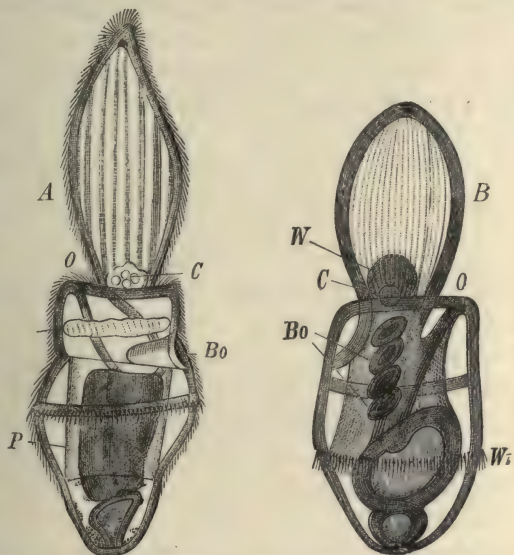


FIG. 78.—Two later stages in the development of *Tornaria* larva, side view. *A* larva with one pair of gill apertures (after Metschnikoff); *B* larva, with four pairs of gill apertures (after A. Agassiz); *Bo* gill apertures; *C* heart; *O* mouth; *P* coelomic sac; *W* rudiment of proboscis-coelom.

such as the presence of eye-spots and an apical plate, does not nullify this resemblance and renders it extremely probable that the Enteropneusta have affinities with the Echinodermata as well as with the Vertebrata—a view which is expressed in this work by the juxtaposition of the chapters dealing with them.

The Balanoglossida live in sand or mud* and are found in most seas. Their burrows, the walls of which appear to be cemented into some consistency by the mucus which the animal secretes, appear frequently to be **U**-shaped, opening on the surface at two points. At one of the openings the casts formed by their faeces are discharged, while the anterior end is in relation with the other opening. In *Dolichoglossus kowalevskii*, Bateson describes them as being highly coloured (collar a bright orange) and as living at about a depth of eight inches with the anterior end of the body (to the branchial region) and the hind end both vertical, the middle portion being coiled in a corkscrew spiral.

They usually possess a disagreeable smell, described as resembling that of iodoform or sometimes that of chloride of lime with a faecal admixture.

It frequently happens that two species live in association: thus Willey records that *Glossobalanus ruficollis* inhabits the same burrow as *Bal. carnosus* in New Britain, while the latter is taken with *Spengelia porosa* at Lifu. They actively burrow in the sand by means of their proboscis and collar, in which the chief muscular development occurs, drawing the hinder part of the body passively after them. The proboscis and collar can be readily rendered turgid or the reverse, and they clear out the sand and mud by swallowing them. Thus their locomotion and alimentation are effected by the same means. It is probable that the inflation of the proboscis and collar which appears to be a necessary condition of their use in locomotion is effected by the taking in of water through the proboscis and collar pores.

The body very readily breaks into pieces—particularly the hinder part, and some species appear to be able to practise autotomy. In presence of this fragility of body, we should expect the power of **regeneration** to be considerable, and this appears to be the case. Animals are frequently taken showing

* See, however, note on p. 103.

features which are only explicable on the view that injuries are being repaired. Thus individuals are found with a very small proboscis and collar, or with an imperfectly formed collar indicating that these parts are being regenerated.

It is asserted that in the regeneration of the collar of *Ptychodera flava* the collar nerve cord is formed as an open groove which is gradually constricted off, and that in the regeneration of the proboscis of the same species the proboscis pores may be equal in size. The first fact has its counterpart in some tornaria larvae in which the medullary cord arises by the constriction off of an open groove, but the latter has no counterpart so far as is known in the early developmental history, no tornaria being known with two water-pores.

Various parasites (Gregarines, flagellate Protozoa, Trematodes, Nematodes, etc.) are found in the Balanoglossida, the most remarkable perhaps being a parasitic Copepod *Ive balanoglossi* sometimes found in the genital pleuræ.

The Balanoglossida are remarkable for the complexity of their structure in contrast with the simplicity of their mode of life and the absence of organs of special sense. There are no known organisms, whether animal or vegetable, at present living, which present such complexity of organization combined with such simplicity of habits. They possess all the three features of the Chordata (see vol. 2, ch. i.) : namely a notochord developed from the dorsal wall of the enteron ; a tubular central nervous system ; and paired branchial apertures leading outwards from the anterior part of the alimentary canal. In addition they possess complex vascular and muscular systems, and a coelom which, largely filled up by muscular and connective tissue in the adult, consists of three main divisions, viz. an unpaired chamber in the proboscis, two paired chambers in the collar, and a similar number of chambers in the trunk.

All the mesodermal structures including the gonads develop from the walls of the coelomic sacs, but no relation has as yet been traced between the cavities of the gonads and those of the coelom. There is no relation between the repetition of any of the organs and that of the coelomic sacs. Indeed all the repeated structures of the adult, viz. the gill-slits and the gonads occur in the region of the posterior or trunk sacs. Although there is no regularity in this repetition it is interesting that it should occur here, for it is these posterior sacs which in *Amphioxus*

and possibly in the Vertebrata become segmented into the mesoblastic somites.

Finally, we must not forget to call attention to the great variability presented by different members of the group. This variability not only occurs among different species, but is also shown by different individuals of the same species. Moreover, and this is the remarkable point, it affects features of structure which to judge by the standard of higher Chordata are of great importance, and are usually perfectly constant through large groups. In illustration of this we may call attention to the condition of the central canal and dorsal roots in the nerve cord of the collar (many species of *Ptychoderidae*), to the canals and pores which connect the proboscis coelom with the exterior (species of *Ptychodera*), and to the length of the branchial region as compared with the rest of the body (macro- and brachybranchiate varieties of *Ptychodera*): these features are variable in some cases within the limits of the same species. As examples of characters which vary in allied species and which we should otherwise judge to be important, we may refer to the presence or absence of liver diverticula, to the condition of the notochord, and to the presence or absence of external protective covering of the gill-slits, and finally to the presence or absence of genital pleuræ. It is in consequence of this remarkable variability that in our treatment of the group we have entered into much greater detail than has been our custom in this work.

Fam. 1. **Ptychoderidae.** Proboscis usually shorter than the collar; cornua of proboscis skeleton do not extend backwards beyond the middle of the collar. Dorsal unpaired roots unite the medullary cord of the collar with the epidermis. Efferent vessels of proboscis united in one transverse plane by a circular vessel with the ventral blood vessel of the collar. Pharyngeal spaces contain circular muscles and completely surround the buccal cavity continuously up to the level of the mouth opening. Perihæmal cavities without transverse muscles. Circular muscles outside the longitudinal are usually present in the body wall of the trunk. Hypopharyngeal streak as a well-marked groove on the ventral side of the pharynx (Fig. 61). Genital pleuræ well developed or small. Lateral mesenteries present in the trunk coelom. External liver-sacculi present (except in *Glossobalanus ruficollis*, Willey). *Ptychodera* Esch., the gill-slits open directly to exterior and the genital pleuræ have a ventral origin, generally with continuous axial canal in the medullary cord of the collar, *Pt. flava* Esch., *erythraea* Speng., *bahamensis* Speng. *Balanoglossus* D. Chi., gill-slits open into pouches which discharge to exterior by dorsal gill pores, genital pleuræ with dorsal origin, *B. apertus* Speng., *clavigerus* D. Chi., *gigas* F. v. Müll., *aurantiacus* Girard, *australiensis* Hill, *carnosus*

Wiley, *biminiensis* Wiley, *jamaicensis* Wiley. *Glossobalanus* Speng., gill apertures as in *Balanoglossus*, genital pleuræ reduced to ridges, *Gl. minutus* Kow., *sarniensis* Koehler, *hedleyi* Hill, *ruficollis* Wiley.

Fam. 2. **Glandicipitidae**. Proboscis longer than collar. Notochord frequently produced anteriorly into a vermiform process. Cornua of proboscis skeleton extend to posterior region of collar. Nerve-roots absent or vestigial. Efferent vessels of proboscis pass obliquely downwards to posterior end of collar. Peripharyngeal spaces separate, vestigial or absent. Periaermal cavities contain transverse muscles. Circular muscles of body-wall lie inside the longitudinal muscles. Genital pleuræ and lateral septa of trunk coelom absent. External liver sacculæ present or absent. *Schizocardium* Speng., right and left peripharyngeal cavities and synaptacula present, ventral septum of proboscis extends to end of vermiform process, external liver sacculæ present, medial gonads absent, pericardial auricles highly developed, hypopharyngeal streak of pharynx reduced to narrow band (Fig. 63); *Sch. brasiliense* and *peruvianum* Speng. *Spengelia* Wiley, peripharyngeal cavities and synaptacula as in *Schizocardium*, ventral septum of proboscis does not extend to the vermiform process, external liver sacculæ absent, medial gonads present or absent, pericardial auricles reduced (Fig. 64), dermal pits in the genital region, hypopharyngeal groove deep and well marked as in *Ptychodera*; *Sp. porosa* and *alba* Wiley. *Glandiceps* Speng., peripharyngeal cavities and synaptacula absent, ventral septum of proboscis and external liver sacculæ and medial gonads as in *Sp.*, pericardial auricles reduced, hypopharyngeal streak of pharynx reduced to broad tract (Fig. 63); *G. talaboti* and *hacksi* Marion, *G. abyssicola* Speng. *Willeyia* Punnett, branchial part of pharynx small compared with ventral portion, without dermal pits, synaptacula, medial gonads.

Fam. 3. **Harrimaniidae**. Boreal forms with large eggs and direct development, vermiform process of notochord and dorsal roots of medullary cord absent; cornua of proboscis skeleton, efferent vessels of proboscis and periaermal cavities as in *Glandicipitidae*; periaermal spaces present or absent; no circular muscles in body-wall of trunk; synaptacula and external liver sacculæ absent. *Harrimania* Ritter, proboscis short, proboscis pores paired, peripharyngeal spaces absent, medial gonads present; *H. kupfferi* v. Will.-Suhm; *H. maculosa* Ritter. *Dolichoglossus* [Speng., proboscis long, proboscis pore unpaired, peripharyngeal spaces present, medial gonads absent; *D. kowalevskii* A. Ag., *D. mereschkowskii* N. Wag., *D. sulcatus* * Spengel, with a dorsally grooved proboscis and 10 or 11 pairs of gill-slits; *D. ruber* Tattersall, from west coast of Ireland. *Stereobalanus* Speng., proboscis short, two proboscis pores, two pairs of genital pleuræ.

Fam. 4. **Protobalanidae**.† The coelom preserves its primitive arrangement, is free from mesenchyme and its mesenteries persist. Lateral septa are absent from the trunk, and periaermal and peripharyngeal cavities from the collar. Gonads in a single row. The other characters as in the Harrimaniidae. *Protobalanus* Caullery and Mesnil, *P. koehleri*, 4-6 cm. in length, St. Martin's Bay, Cap de la Hague, north coast of France.

* *Dolichoglossus otagoensis* Benham (*Q.J.M.S.*, 42, 1899, p. 497), a form recently described from New Zealand, creeps on seaweed by means of a very contractile proboscis, which is grooved dorsally as in *D. sulcatus*; it possesses only 12 pairs of gill-slits.

† Caullery et Mesnil, *Zool. Jahrb. Anat.*, 20, 1904, p. 227.

Order 2. CEPHALODISCIDA.

Enteropneusta in which the collar is prolonged into paired tentaculiferous arms and the trunk is much shortened in its antero-posterior axis, with at most one pair of branchial apertures. The animals live in colonies and inhabit tubes which are formed by the proboscis.

The Cephalodiscida comprise two genera, *Cephalodiscus* McIntosh and *Rhabdopleura* Allman. They are colonial animals which possess the power of budding and inhabit tubes secreted by the ectoderm of the flattened proboscis. The two genera while agreeing in most points of structure differ in the presence or absence of branchial apertures. In *Cephalodiscus* there is one pair of lateral openings leading outwards from the pharynx; in *Rhabdopleura* branchial apertures are absent. In the following account the two genera are dealt with separately.

*Cephalodiscus** resembles the Balanoglossids in the main plan of its organization, but differs from them in the fact that the trunk region, though exceedingly shortened antero-posteriorly, is much elongated in the dorso-ventral direction, and in the restriction of certain trunk organs, which are repeated in the Balanoglossida, to a single pair, e.g. gill-slits and gonads. Moreover, it has the power of reproducing itself by budding; and several individuals live in association in a single tube system.

Cephalodiscus was discovered by the *Challenger* in 1876, at a depth of 245 fathoms, in the Strait of Magellan. It has since been found in other localities (Japan, and from comparatively shallow water in the Malay Archipelago and in the Antarctic). It was at first thought to be a compound Ascidian. Then it was referred to the *Polyzoa*, and it was not until 1887 that its structure was satisfactorily elucidated by Harmer and its real nature as an ally of the Enteropneusta demonstrated.

A considerable number of individuals, probably all produced by budding from a single original individual, live together in a system of ramifying, sometimes anastomosing tubes which

* W. C. McIntosh, *Cephalodiscus*, *Challenger Reports*, vol. 20, 1887. S. F. Harmer, Appendix to the preceding. Id., On the Notochord of *Cephalodiscus*, *Zoolog. Anzeiger*. 1897. Id., The Pterobranchia of the Siboga-Expedition, *Siboga-Expeditie*, vol. 26 bis, 1905. A. T. Masterman, On the Structure of *Cephalodiscus*, *Q.J.M.S.*, 40, p. 340, and *Transactions of Royal Soc. of Edinburgh*, 39, 1898. Id., *Q.J.M.S.*, 46, 1903, p. 715.

consist of a flexible, brownish semitransparent material. The tubes are composed of superposed lamellae and are probably secreted by the proboscis of the animal (see below). The organisms are not attached to each other or to the wall of the tube in any way, but appear to have the power of moving freely about inside it. Scattered about here and there on the tubes are large rounded apertures, near which the individuals are often found, and through which they can protrude their tentacular tufts. The tubes are covered with tapering spinous processes of their walls. The cavity of the tube may be continuous or it may be divided up into chambers, one for each individual or zooid. With regard to the size of a colony it may be mentioned that in *Cephalodiscus dodecalophus* the network of tubes covered an area of 9 inches by 6 inches. The stems have a diameter of from 4 to 10 mm., and the whole colony appears to have been attached to marine objects such as stones, sponges, etc., by vertical stems which descend from the underside of the net-

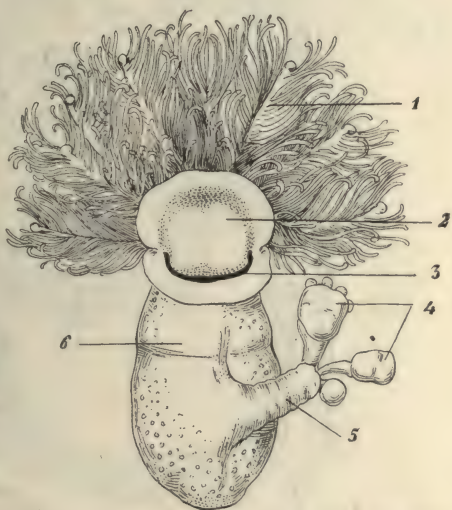


FIG. 77.—*Cephalodiscus dodecalophus*, anterior view (after McIntosh). 1 tentacles; 2 proboscis (buccal shield); 3 pigment band on proboscis; 4 buds; 5 pedicle; 6 trunk.

work to the substratum. The natural position of the colonies would thus appear to be horizontal. The full-grown individuals of *C. dodecalophus* measure about 2 mm. in their longest diameter.

Cephalodiscus may be described as an animal in which the oral axis of the body is very short and the ventral surface behind the mouth is produced into a large hump in which the alimentary canal is continued (Figs. 77, 78). This ventral hump terminates at its ventral and anterior end in a pedicle on which buds are continually being formed.

The mouth is ventral and anterior and is overhung by a large

preoral lobe (Figs. 77, 2, 78, 18) called the **buccal disc** or **proboscis**. Behind this there is a region of the body which, except in the young bud, is not very distinctly marked off either from the proboscis in front or from the trunk behind. This is the **collar** region.



FIG. 78.—Median longitudinal vertical section through *Cephalodiscus dodecalophus* (after Harmer, from Lang). The figure is diagrammatic, especially in the fact that certain structures not in the middle line are shown. 2 nervous system; 3 collar coelom; 5 postoral lamella (operculum); 8 trunk coelom; 9 pharynx; 10 oesophagus; 11 stomach; 12 intestine; 13 buccal cavity; 14 pedicle; 15 ovary; 16 anus; 17 oviduct; 18 proboscis (buccal shield); 19 proboscis coelom; 20 one of the proboscis pores; 21 notochordal diverticulum of the pharynx.

The collar forms no projection round the base of the proboscis in the mid-dorsal region, but its ventral and lateral portions project forward, forming a kind of lip (Figs. 78, 79). This lip is called the **operculum***: it forms the ventral and lateral edge of the

* The operculum can be folded backwards, a peculiarity which combined with the inconspicuousness of the ventral part of the collar has led some authors to describe it as a projection of the posterior edge of the collar.

mouth-opening which lies between it and the base of the proboscis stalk. The arms are prolongations of the dorso-lateral parts of the collar commencing at the point where this lip-like projection passes into the dorsal part of the collar. They are tentaculiferous and vary in number from four to six pairs (one pair in the males of *C. sibogae*). In *C. dodecalophus* they are slightly swollen at their extremities.

Each arm contains a prolongation of the collar body-cavity (Fig. 79) and is grooved on its ventral surface, the grooves uniting in pairs and converging to the corners of the mouth, near which they terminate.

The ectoderm of the swellings at the end of the arms of *C. dodecalophus* contains a number of ovoid globules of a clear substance which have been variously interpreted as organs akin to the rhabdites of Turbellaria, and as the refractive structures of a rudimentary visual organ. Similar refringent vesicles are found along the whole course of the arms of the males of *C. sibogae*.

Behind the collar region is the trunk, the ventral portion of which is prolonged into the huge hump before referred to. The single pair of gonads (Fig. 78, 15) are placed in the anterior part of the trunk, just behind the collar, and open dorso-laterally one on each side. The anus is at the hind end of the dorsal surface (Fig. 78, 16). The proboscis presents a broad disc-like surface towards the front (Fig. 77) and is marked by a crescentic band of pigment in its ventral portion (3). Its anterior wall is covered with a glandular ectoderm, which appears to play some part in the formation of the tube, as in *Rhabdopleura*. The mouth is on the ventral side at the junction of the proboscis and collar (Fig. 78)

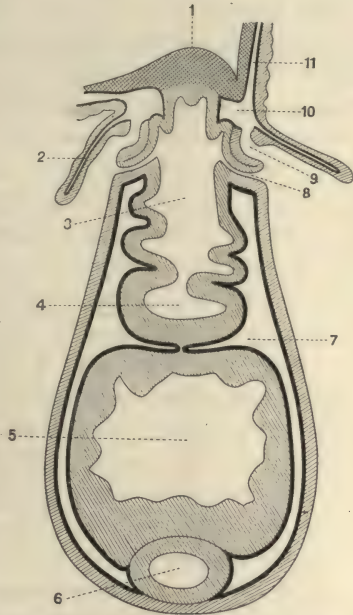


FIG. 79.—Transverse section through *Cephalodiscus dodecalophus* (after Harmer). 1 central nervous system of the collar region; 2 operculum turned backwards; 3 pharynx; 4 oesophagus; 5 stomach; 6 intestine; 7 trunk-coelom; 8 gill-slit; 9 collar-pore; 10 collar-coelom; 11 arm.

and is usually entirely hidden by the ventral portion of the overhanging proboscis.

The alimentary canal (Fig. 78) consists of mouth-cavity, pharynx, oesophagus, stomach, and intestine which opens by the posterior and dorsal anus. The bulk of it is contained in the great ventral hump so characteristic of this animal.

The anterior end of the pharynx gives off a forward diverticulum which extends through the collar region into the proboscis : this is the **notochord** (Fig. 78, 21). There are two **gill-slits**, one on each side leading outward from the pharynx and opening ventro-laterally on the anterior part of the trunk. The body-cavity is arranged as in other *Enteropneusta*, i.e. it consists of an unpaired chamber in the proboscis which opens to the exterior by a pair of pores at the junction of the proboscis and collar region of the body (Fig. 78, 20) ; of a pair of chambers in the collar region, which also open outwards by a pair of collar pores (Fig. 79, 9), and of another pair in the trunk which are in relation with the greater part of the alimentary canal and with the ovaries, and which do not open to the exterior. The two halves of the body-cavity of the collar overlap dorsally the hinder part of the proboscis region (Fig. 78, 3). The dorsal and ventral mesenteries appear to persist, completely or incompletely, in the collar and trunk regions. The sexes are separate and all the individuals of one colony are of the same sex (except in *C. nigrescens*, p. 109). The ovaries are paired sacs placed dorsally in the anterior part of the trunk region. They open to the exterior by two short oviducts, the walls of which are richly pigmented (Fig. 78, 17). The male colonies appear, in some species (e.g. *sibogae*), to be dimorphic, containing male individuals which are characterized by possessing two arms without tentacles, a long pedicle and an abortive alimentary canal, and neuter individuals which are like the females but without ovaries. The coelom of the proboscis and collar are to some extent obliterated by muscle and connective tissue, as is the prolongation of the trunk body-cavity in the pedicle. The organs appear to be separated by a basement membrane as in the Balanoglossida and there is no connective tissue of the usual kind except in the coelomic sacs in the dorsal region of the collar. The central nervous system is contained in the ectoderm. It extends forwards on to the hinder part of the proboscis and the proboscis pores perforate its

anterior portion (Fig. 78). It is moreover continued as a nervous tract along the dorsal side of each arm.

The pedicle is a process from the ventral surface. It is said to be largely filled with longitudinal muscular fibres, but it appears to contain a prolongation of the posterior body-cavity. Buds are formed upon its terminal portion. From one to three buds are found upon almost all full-grown individuals. The endodermal tissues of the parent do not extend into the pedicle and play no part in the formation of the bud, the alimentary canal of the latter being entirely formed by an invagination of ectoderm.

Cephalodiscus has, in its proboscis and in close contact with the notochord, structures corresponding to the pericardial sac, glomerulus, and central blood-sinus (heart) of the *Balanoglossida*.

The pericardial sac is at the anterior end of the notochord and contains the heart in its interior. Blood vessels have been made out in other parts of the body as spaces the walls of which are probably formed by the walls of the mesodermic cavities, or they may be spaces between the same structures and the ectoderm or endoderm.

Free eggs and embryos are found in the tubes of some species. The ova are of a fair size and contain a considerable quantity of yolk. The cleavage is complete and the embryos leave the colony at an early stage as ciliated planulas.

The following species are known. *C. dodecalophus* M'Intosh, with 12 arms, with end bulbs and vesicles; cavity of tube continuous; Straits of Magellan, 448 metres. *C. levinseni* Harmer, with 12 arms, without end-bulbs or vesicles; cavities of the tubes divided up into chambers, one for each zooid; sea between Japan and Corea, 183 metres. *C. gracilis* Harmer, very small; with 10 arms, apparently without end-bulbs and vesicles in adult; E. coast of Borneo, reef. *C. sibogae* Harmer, male-colony only known, with dimorphic individuals (see p. 108); S.E. of Celebes, 75-94 metres. *C. nigrescens* Lankester,* colony large and massive, nearly transparent, with tubes projecting from its surface, each tube being cut off from the rest and containing one full-grown zooid; the zooids are deeply pigmented and large (4.5 mm. \times 1 mm.) and have 6 to 8 pairs of arms which are without terminal swellings; each colony contains male, female, and hermaphrodite individuals, the latter having one ovary and one testis; Antarctic Ocean, in 100 fms.

The genus *Rhabdopleura*† Allman must also, in view of Fowler's

* *Proc. Roy. Soc.*, 1905, 76 B, p. 400.

† Allman, *Q.J.M.S.*, 9, 1869, p. 57. Sars, *Q.J.M.S.*, 14, 1874, p. 23. Lankester, *Q.J.M.S.*, 24, 1884, p. 622. Fowler, *Proc. Roy. Soc.*, 52, 1893, p. 132, also in *Leuckart's Festschrift*, Leipzig, 1892, p. 293, and *Q.J.M.S.*, 48, 1904, p. 23. Schepotieff, A. Zur Organisation von *Rhabdopleura*, *Bergens Museums Aarbog.*, 1904, No. 2, and *Zool. Anzeiger*, 28, 1905, p. 795.

work, be placed in alliance with the Enteropneusta. It differs, however, from the other members of the phylum by the absence of pharyngeal apertures.

It exists in the form of colonies, the zooids of which are con-

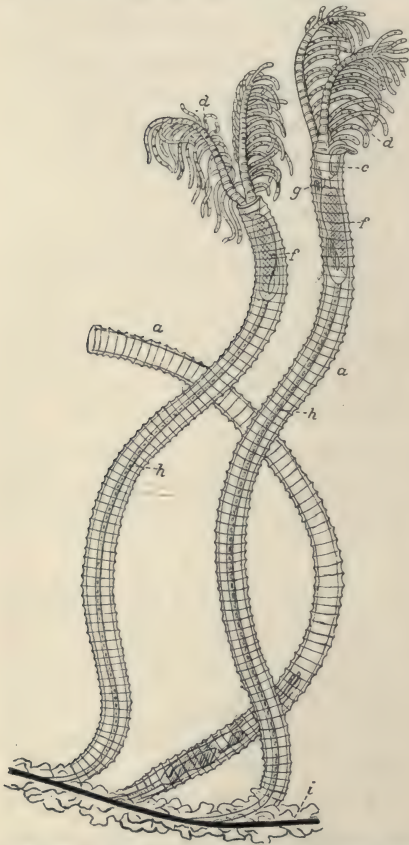


FIG. 80.—Portion of a living colony of *Rhabdopleura normani* (Allman), Lofoten Islands. $\times 10$. *a* the terminal branches with the zooids in different states of protrusion; *c* the proboscis (cephalic disc); *d* the two tentacular arms; *f* the stomach; *g* the intestine; *h* the stalks of the zooids; *i* the axial rod in the creeping stolon.

nected with one another by living substance and are contained in transparent tubes of a chitin-like material. The colonies have the form of a branching axis which lies upon the substratum and gives off at irregular intervals the terminal branches. These, for the most part, after adhering for a short distance to the substratum, rise up and project freely into the water. At their free ends are found the openings of the tubes by which the zooids come into relation with the external world. The zooids consist of a body and a stalk (Fig. 81). The body is small (12 mm. in diameter) and possesses at its anterior end a preoral lobe—the buccal disc or proboscis, a pair of tentaculiferous arms arising laterally at the level of the mouth from the collar region (see

below), a mouth on the ventral side of the buccal disc (Fig. 82, 8) and an anus (3) placed at about the same level as the mouth on the dorsal side. The stalk is the narrow ventral end of the body which passes down to join the common axis of the colony in the creeping stolon. Its connexion with the body is somewhat an-

teriorly placed. The tube is secreted by the buccal discs of the zooid. It consists of a series of rings, each of which is secreted separately by the buccal disc and added to its predecessor. It is therefore quite independent of and separate from the bodies and

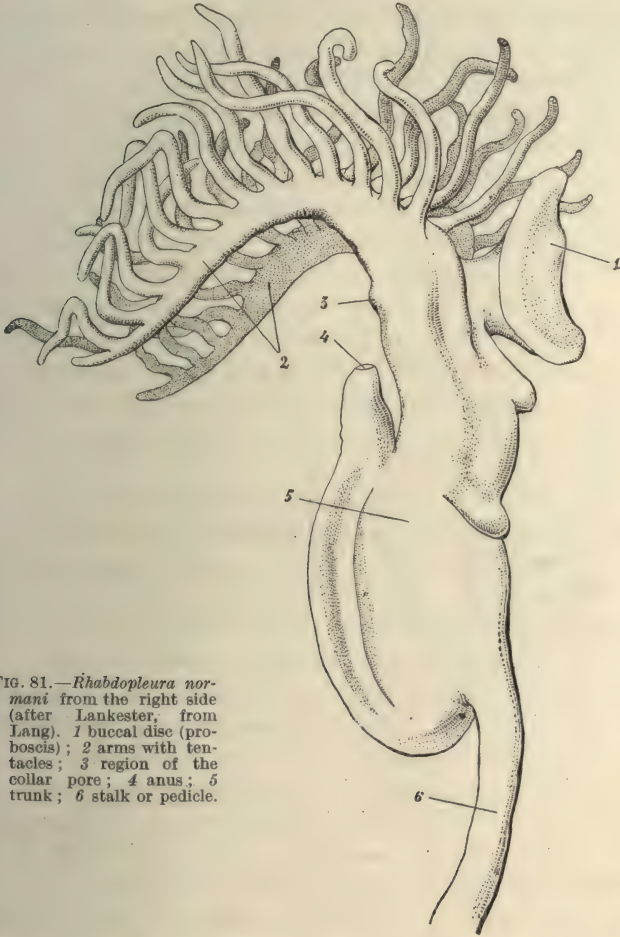


FIG. 81.—*Rhabdopleura normani* from the right side (after Lankester, from Lang). 1 buccal disc (proboscis); 2 arms with tentacles; 3 region of the collar pore; 4 anus; 5 trunk; 6 stalk or pedicle.

stalks of the zooids, and the body of the animal can move freely within its tube. It can be retracted into the tube by the contraction (into a spiral) of a muscle in the stalk, and it can crawl up the inside of its tube by help of its buccal disc and can protrude its arms from the terminal opening.

The common axis consists of the stalks of the zooids in earlier stages of the growth of the colony. It lies within the tube and the older parts of it possess a cuticle on its ectoderm. This cuticle becomes hardened and of a dark colour. It fuses secondarily with one side of the wall of the tube and forms a conspicuous object as a dark brown, thin rod easily visible to the naked eye in the creeping stolon of the colonies. Some of the terminal branches of the colony do not rise up, but the tubes with their contained axis continue along the substratum and end in open mouths. These are actively growing proliferous branches. The axis in them terminates in an imperfect zooid, the proboscis of which adds to the tube, while its stalk has lateral wart-like buds. Transverse septa are formed across the tube between the buds, and the buds increasing in size burst through the wall of the tube and grow outwards from the creeping axis as imperfect zooids. Most of the new zooids so formed rise up and develop into the perfect form; a few no doubt adhere to the substratum and form new proliferous branches. It follows from what has been said that the creeping (stolonic) part of the tube is divided up into chambers by septa which do not however interrupt the continuity of the living substance of the stalk, and from each of which one zooid-bearing branch arises. There are no branchial apertures, but there is on each side a groove, between the insertion of the proboscis and that of the arms, which leads through the mouth into the oesophagus, on the side-wall of which it can be traced. This groove is called the branchial groove.

The anatomy of the animal may be understood at a glance by inspection of Fig. 82. The alimentary canal is bent on itself. The buccal cavity is provided with an anteriorly directed diverticulum which is continuous with a rod-like structure, apparently half-cellular and half-gelatinoid (Fig. 82, 9). This, which is clearly comparable to the notochordal diverticulum of other Enteropneusta, projects into the base of the preoral disc (proboscis). The body cavity, which appears to have a cellular lining, is divided into five chambers arranged as in other Enteropneusta; viz. an unpaired chamber (10) in the preoral disc (proboscis), a pair of chambers separated from one another by dorsal and ventral median septa and placed in what may be called the collar region of the body (Fig. 82, 2), and finally a pair of chambers in the trunk in relation with the greater part of the alimentary

canal (4). The collar-cavities are continued into the arms, which arise from the collar region, and the trunk cavities appear to be continued into the stalk. At any rate the stalk contains in addition to its muscular tissue two cavities separated by a septum.* The proboscis-cavity possesses a pair of pores, and the collar-cavities communicate with the exterior, each by a collar canal. On the dorsal side of the collar region behind the collar coelom (Fig. 82), there is an ectodermal thickening which seems to correspond with the nerve plate of *Cephalodiscus* and the medullary nerve cord of the Balanoglossida.

Mesoblastic skeletal tissue, apparently similar in character and relations to that of the Balanoglossida, occurs in the arms and tentacles, and in the axis of the stalk.

Most of the specimens hitherto found have been devoid of generative organs, but in a few there was a testis in the form of an elongated sac lying parallel to the intestine on the right side, and forming a projection on the surface of the body; it opened close behind the anus.

A vascular system consisting of a dorsal and ventral vessel has been described, and there appears to be a pericardial vesicle and heart at the anterior end of the notochord as in other Enteropneusta.

Rhabdopleura† is a marine animal and is found in compara-

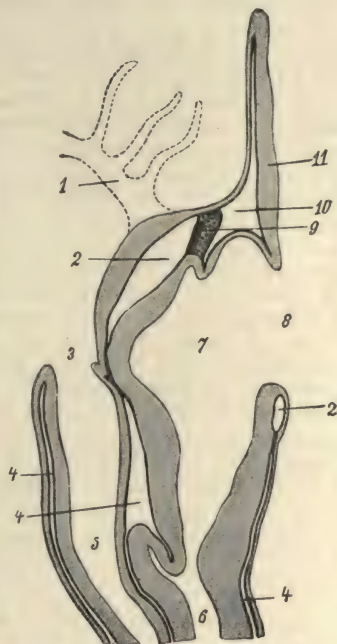


FIG. 82.—*Rhabdopleura normani* in longitudinal vertical section (after Fowler from Lang). 1 arm of one side, indicated by dotted lines; 2 anterior paired (collar) coelom; 3 anus; 4 posterior paired (trunk) coelom; 5, 6 alimentary canal; 7 buccal cavity; 8 mouth; 9 anterior diverticulum of buccal cavity (notochord); 10 anterior unpaired (proboscis) coelom; 11 buccal shield.

* Fowler thinks that the stalk contains a cord of endoderm which is continuous with that of the alimentary canal. If this is so, the endoderm may participate in the budding.

† It has been suggested that the section of the Graptolites known as *Monograptidae* are nearly related to *Rhabdopleura* (see Allman, On the Morphology and Affinities of Graptolites, *Ann. and Mag. Nat. Hist.*, 1872, and Schepotieff, *Neues Jahrbuch f. Mineralogie*, 2, 1905, pp. 79-98).

tively deep water (40 to 120 fms.). It is widely spread, having been recorded from the Norwegian Fiords, off the Lofoten and Shetland Islands, off Tristan d'Acunha, South Australia, the Malay Archipelago, the Azores, Ireland and Brittany.

The question of the relationship of *Phoronis* to the Enteropneusta was dealt with on p. 547 of vol. i. of this work. Since that passage was written several memoirs * dealing with the development and structure of the Actinotrocha larva have been published. The upshot of these is to justify the criticism there set forth. To take the points *seriatim*, the existence of a "neuropore" and "subneural gland" has not been confirmed: on the contrary it has been denied by Ikeda and Goodrich. The relations of the stomach cæcum of Actinotrocha have been shown to be not those of a notochord. No evidence is forthcoming to contradict Caldwell's original statement that the cavity in the preoral lobe of Actinotrocha is haemocoelic (so-called primary body cavity of the trochosphere), and not a coelomic sac. It seems fairly clear that nothing comparable to proboscis pores or to collar pores are present. The only new point that has come out in this connexion is that the preseptal body-cavity of the adult is present in the old larva as a horseshoe-shaped cavity which underlies the ring of tentacles and send extensions into them, but the development of this cavity has not been ascertained. Finally, it has been shown that Caldwell was right in his account of the larval excretory organ as a ciliated canal not opening into the body-cavity, but terminating internally in some peculiar cells which recall the so-called flame cells of Platyhelminthes and Annelid larvae, etc. (solenocytes of Goodrich, see vol. 2., pp. 27, 28).

* Masterman, *Q.J.M.S.*, 43, 1900, p. 375. Ikeda, *Journ. Coll. Sci. Imp. Univ. Japan*, 13, 1900-1, p. 507. Goodrich, *Q.J.M.S.*, 47, 1903, p. 103. Schultz, *Z. f. w. Z.*, 75, 1903, pp. 391, 473. M. de Selys Longchamps, *Mém. Classe Sci. Acad. Belgique*, i. 1904.

CHAPTER III.

PHYLUM ECHINODERMATA*

With a radial, usually pentamerous arrangement. The body-wall contains calcareous plates and generally bears spines. The coelom is divided into two well-marked portions—the perivisceral cavity and the watervascular system, and the gonads are not connected with it in the adult.

The Echinodermata, like the Coelenterata, present a radial arrangement of their principal organs and were for that reason united by Cuvier with the polyps and medusae in the group *Radiata*. With the progress of anatomical knowledge, it soon became apparent that the organization of the Echinoderms differs totally from that of the Coelenterates and belongs to a much more complex grade of development. This fact, which was first recognized by R. Leuckart, led to the separation of the two groups and to the establishment of two independent phyla, the Coelenterata and Echinodermata. A trace of the old view

* Fr. Tiedemann, *Anatomie der Röhrenholothurie, des pommeranzfarbenen Seesternes u. des Steinseeigels*, Heidelberg, 1820. De Blainville, *Manuel d'Actinologie*, Paris, 1834. L. Agassiz, *Monogr. d'Echinodermes vivants et fossiles*, Neuchâtel, 1838–42. L. Agassiz et E. Desor, "Catalogue raisonné des familles, des genres et des espèces de la classe des Echinodermes," *Ann. Sci. nat.* (3), 6, 7, and 8, 1846–7. E. Forbes, *A History of British Starfishes*, London, 1841. R. Leuckart, *Ueb. d. Morphologie u. Verwandtschaftsverhältnisse d. wirbellosenthier*, Braunschweig, 1848. J. Müller, "Ueb. d. Bau d. Echinodermen," *Abh. d. Berlin Akad.*, 1853. *Id.*, "Sieben Abh. ü. die Larven u. d. Entw. d. Echinodermen," *Abh. d. Berlin Akad.*, 1846, 1848, 1849, 1850, 1851, 1852. A. Agassiz, "On the Embryology of Echinoderms," *Memoirs of the American Academy*, 1864. E. Metschnikoff, "Studien ü. die Entwicklungsgesch. der Echinodermen u. Nemertinen," St. Petersburg, 1869. H. Ludwig, "Morphologische Studien an Echinodermen," *Z. f. w. Z.*, 1876–82. *Id.*, "Echinodermen," in "Bronn's Klassen u. Ordnungen," in progress. O. Hamann, "Beiträge z. Histologie d. Echinodermen," *Jena. Zeitschrift.*, 1884–89. L. Cuénot, "Études morphologiques sur les Echinodermes," *Arch. de Biologie*, 11, 1891. H. E. Durham, "On Wandering Cells in Echinoderms, etc.," *Q.J.M.S.*, 33, 1892. P. H. Carpenter, several memoirs in the *Q.J.M.S.* and other Journals, 1875–1890. E. Ray Lankester, *A Treatise on Zoology*, Pt. 3, *The Echinoderma*, London, 1900. E. W. MacBride, Echinodermata, in vol. I of the *Cambridge Natural History*, 1906.

has until quite recently survived in the juxtaposition of the two phyla which used frequently to be found in works on Zoology and Comparative Anatomy. But of late years it has been recognized more and more clearly that this juxtaposition is not warranted by the facts and that the affinities of the Echinodermata, in so far as any can be traced, are rather with the higher phyla of the Metazoa, than with the lower. Expression was given to this view in 1877 by Huxley in his *Anatomy of Invertebrata* and in 1880 by F. M. Balfour, who in his *Comparative Embryology* placed the Echinodermata at the end of the volume dealing with the invertebrate groups, in the neighbourhood of the Enteropneusta and Chordata. This example was followed in 1890 by A. Lang in his textbook of Comparative Anatomy, and now we, in the light of the most recent work on the subject, have thought it right to take the same course.

The Echinodermata are radiately symmetrical animals (see p. 117) in which the number of radii is nearly always five or some multiple of five. This symmetry is, however, characteristic of the adult only, for in the youngest state all members of the group are bilaterally symmetrical and in nearly all there is a free-swimming bilateral larva. The view usually taken and adopted by us when referring to the matter in the chapter on Mollusca in the first volume of this work (p. 317) is that the bilateral symmetry is the primitive symmetry possessed by some adult ancestor and that the radial arrangement is to be regarded as a distortion from the original condition. Now, however, after a more complete study of the group, we see reason to suspend our judgment on this matter, and though we should hesitate to adopt the view that the Echinodermata have been derived from asymmetrical or from radiately symmetrical forms, and that the larva has been especially produced and modified for a free-swimming life, we are of opinion that there is at least as much to be said for it as for the older and more usually adopted view that the ancestral form was a form in which bilateral symmetry had been completely evolved.*

The radial symmetry is expressed not only in the external appearance, but also in the arrangement of most of the internal organs. It is, however, never completely carried out, and in

* For a discussion of this question, see the section on "Affinities," p. 160.

some forms (certain Echinoids) there is a tendency to bilateral symmetry. Speaking generally the body may be described as spherical or discoidal in form, with the mouth in the centre of the lower * surface and the anus at or near the centre of the upper surface. An oral and aboral surface or pole may thus be distinguished. The anus varies more in position than does the mouth. The mouth is nearly always in the centre of the oral surface or at the oral pole ; in a few Holothurians, some Echinoids and in *Actinometra* among Crinoids it is slightly shifted from this position. The anus on the other hand is central only in Holothurians, and even in some of these it is slightly displaced ; in Asteroids and regular Echinoids it is very near the centre of the aboral surface, but always slightly excentric ; in irregular Echinoids it is at some distance from the central point and sometimes on the oral surface ; and in Crinoids it is always on the oral surface. In a few Asteroids (*Astropectinidae*, etc.) and all Ophiuroids the anus is absent in the adult.

The radial structure is indicated externally by the rows of tube-feet (p. 129) which extend outwards from the mouth towards the aboral pole. The surface of the body is thus marked into **radii** along which the tube-feet are arranged, and into **interradii**—the portions between the tube-feet rows. In Asteroids, Ophiuroids, and Crinoids the radial portions of the disc are prolonged into processes, which constitute the arms ; in Holothurians and Echinoids the radii are not so prolonged and there are no arms. The rows of tube-feet never extend quite to the aboral pole ; it is therefore possible to distinguish that portion of the surface of the body from which tube-feet project, as **ambulacral** or **actinal**, from the **antambulacral** or **abambulacral** or **abaetinal** surface which is without tube-feet. In the brachiote Echinoderms, that is in Asteroidea, Ophiuroidea and Crinoidea, these two regions or surfaces are about equal in extent, the whole of the oral surface being ambulacral, and the whole of the aboral surface antambulacral. In such cases it is customary to call the lower or ambulacral surface ventral, and the upper or antambulacral surface dorsal. But it is better not to use the terms dorsal or ventral in adult Echinoderm morphology without prefixing the word adult, because dorsal and ventral are used

* In Crinoids and their allies the oral surface is turned upwards in the natural position of the animal.

in an entirely different sense in describing the larvae and in adult Holothurians, and cannot be used satisfactorily in Echinoids at all. In Holothurians and Echinoids the tube-feet extend almost to the aboral pole, and the antambulacral surface of the body is restricted to the very small region round the anus. Moreover in Holothurians, in which the body is cylindrical and lies with its whole length applied to the substratum, it is usual to call one surface of the cylinder, viz. that on which the single genital opening and madreporite are placed, the dorsal, and the other side the ventral. In many Holothurians the animal always lies with the three radii (*trivium*) of the so-called ventral surface directed towards the substratum and uses the tube-feet of these radii for adhesion, the tube-feet of the two dorsal radii (*bivium*) being without suckers and probably used for respiration and sensation only. In pentameral Echinoderms the words *bivium* and *trivium* are frequently used to designate the two groups into which the five radii may be divided. These words are used however in a somewhat vague sense and it must not be supposed that the arms of the bivium and trivium of one class are necessarily the same as the bivial and trivial arms of another class. The water-pore or madreporite is generally single and always interradiial in position. It is generally abactinal, but in Crinoids and Ophiuroids it is on the ambulacral surface. In Holothurians the madreporitic interradius occupies the middle of the so-called dorsal surface.

In Ophiuroids as in Asteroids the water-pore is generally single, but in Crinoids it is always multiple, there being one (*Rhizocrinus*) or more than one in each interradius. The number of water-pores (madreporites *) is however subject to variation in all classes of Echinoderms except Echinoids, in which normally there is never more than one.

In Echinoids, Holothuroids, Neocrinoids and Blastoids the number of radii is constantly five except in abnormal individuals.† In Asteroids, Ophiuroids, Crinoids and Cystids this number may

* For complete explanation of the terms water-pore and madreporite see below, p. 127. It may be mentioned here that the numerous perforations in the madreporitic plate of Echinoids and Asteroids represent one water-pore only.

† See Bateson, *Materials for the Study of Variation*, London, 1894, p. 432 et seq. In Echinoids 4- and 6-rayed abnormalities are not uncommon, and in Holothurians Ludwig found half a dozen 6-rayed individuals in 150 specimens of *Cucumaria planici*.

be departed from.* In most cases the number of radii is determined early in development, but in a few forms (e.g. *Labidiaster*) the number increases with the growth of the animal, at any rate in the early stages of the adult (Perrier). In Cystids the number of radii varies more than in any class, the number two or three sometimes occurring.

Enumeration of Radii. After some hesitation we have decided to adopt a definite enumeration of the radii for all classes of Echinoderms. Our enumeration, which is shown in Fig. 83, is based on the assumption that the position of the stone-canal and primary water-pore is the same in all classes. If that assumption is incorrect, which it may very well be,† the homologies which might be deduced from it fall to the ground. In any case we desire to warn the reader against attaching too much importance to the determination of homologies based solely on this assumption. We have adopted the enumeration because it conduces to clearness and enables us to impart a greater precision to our descriptions and not because we think that it is of any importance from the point of view of determining homologies.

The interradius in which the hydrocoel closes in the larva presents remarkable variations, in relation to the position of the madreporite, as the diagram indicates, and it is probable that later researches will show an even greater variability in this respect, the number of species hitherto examined from this point of view being small.

Our enumeration is identical with that of Lovén excepting in its application to Crinoids (see p. 272). The first-formed water-pore of Crinoids and the anus are in the same interradius. As our enumeration is based on the position of the water-pore, we assign the anus of Crinoids to interradius II, III, and not to interradius I.V, as is done by Lovén.

One of the most important characteristics of the Echinodermata is the presence of calcareous plates in the dermis. These may have various forms, from the isolated plates and

* In Ophiuroids and Crinoids, though the number of radii is usually five, the arms in some cases branch.

† It is quite likely, as suggested by MacBride, that the interradius of closure is the fixed point, the position of the madreporite being variable. He points out to me that the stone-canal opens on the inner side of the hydrocoel ring, and that the position of the opening might easily shift. The madreporite being on the dorsal surface might also easily change its interradius, as the anus undoubtedly does.

spicules of Holothurians, which are remarkable for their definite and symmetrical form, to the compact and complete dermal skeleton of Echinoids. The plates arise as deposits in the form

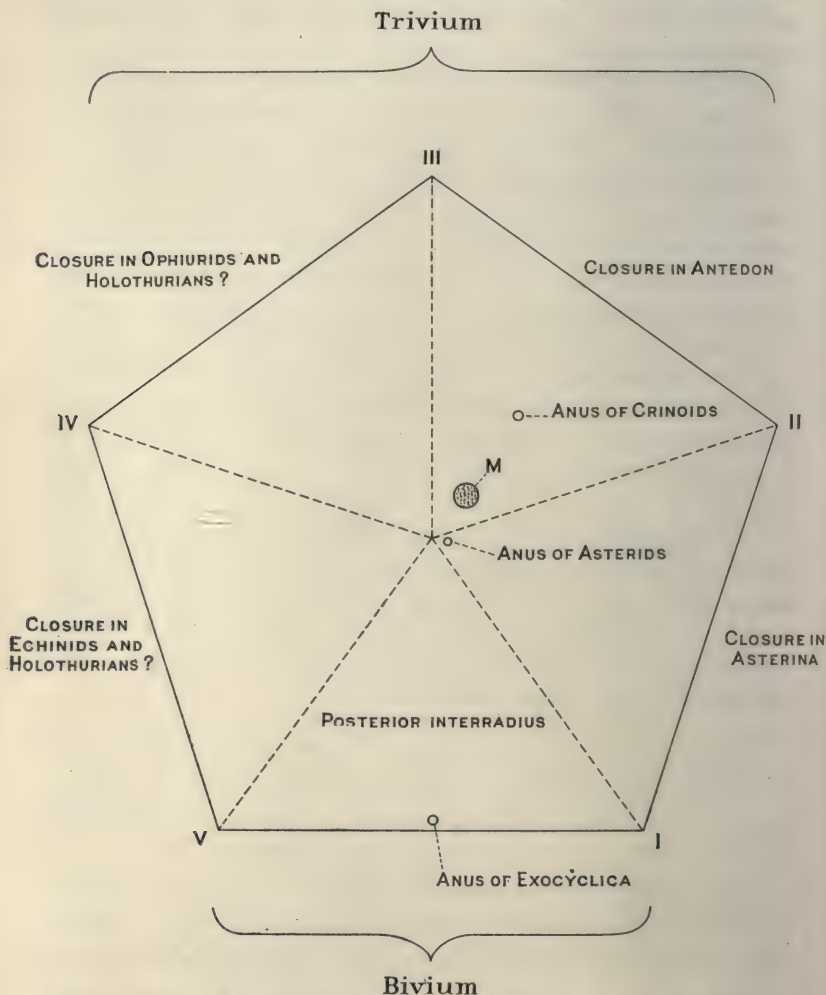


FIG. 83.—Diagram of an Echinoderm viewed from the aboral pole, to show the enumeration of the radii adopted in this work. The diagram also shows the interradius in which the hydrocoel closes in certain observed cases (vide Bury, *Q.J.M.S.*, 29, p. 431). I-V the radii; M the madreporite. In MacBride's enumeration of the hydrocoel lobes adopted here in the succeeding account of the development of *Asterina*, lobe no. 1 is radius II, lobe no. 2 is radius III, and lobe no. 5 is radius I. In Cuénot's enumeration the equivalence is A=V, B=I, C=II, D=III, and E=IV. Radius I is the right anterior, and radius IV is the left anterior radius of Crinoids. The plane of symmetry of Holothurians and Crinoids passes through radius V and interradius II. III, that of Asteroids through IV and I-II, and that of exocyclic Echinoids through III and V-I (Lovén's plane of symmetry).

of networks or spongeworks of calcareous matter in the connective tissue. In many of the classes (Asteroids, Ophiuroids and Echinoids) these plates carry spines and processes which project on the surface, and in the young state at least are covered by the epidermis. The majority of the spines are movably articulated with the plates, and in Asteroids and Echinoids some of them are specially modified as snapping organs—the *pedicellariae*. The function of the spines is probably mainly protective, but in the case of the long spines of Echinoids it is locomotory. The *pedicellariae* are protective, seizing foreign organisms (p. 224). They are said not to bite animals of the same species (*autodermophily*, Uexküll).

The epidermis is generally ciliated, but in Ophiuroids, and on the aboral surface of Crinoids it is difficult to distinguish it as a layer distinct from the cutis.

The description of the skeletal system will be best dealt with in connexion with the different classes of the phylum. It will be well however to call attention here to certain plates which are supposed to be homologous throughout the group: these are the plates of the **oral** and **apical systems**. The **oral plates** are five in number and are placed interradially round the mouth on the oral surface. They can be distinguished in many Crinoids and in Ophiuroids, but are not clearly distinguishable in any other class.

The plates of the apical system are placed at the aboral pole, and when present are usually discernible at a comparatively early stage of development. In typical cases (Ophiuroids, Fig. 84, many Crinoids, Fig. 85) they consist of a **central plate** surrounded by ten plates, five of which are radial in position and five interradial: the former are called **infrabasals**, the latter **basals**. Beyond this circle there are five radially placed plates called the **radials**. Of these plates the infrabasals, or *under-basals* as they are sometimes called, are frequently absent. In Echinoids the central plate is not pierced by the anus which is placed on one side of it; moreover it is frequently very difficult to distinguish it, owing to the presence of a number of small plates, called the periproct plates, at the apical pole. In Crinoids the position of the central plate is not certainly known, but it is supposed to be represented by the so-called dorso-central which is found at the peripheral end of the stalk. In Asteroids a complete

apical system can sometimes be made out, but as a rule the plates are indistinguishable from the other plates of the antambulacral surface. In Holothurians the plates of the oral and apical systems are absent both in the larva and in the adult. In Echinoids, in which a central plate can often be made out, the five interradial basals (genital plates) are always present, but infrabasals and radials are not found. The oculars of Echinoids, which are often called radials, are rather comparable to the **terminals**, which must now be referred to. Whereas the plates of the apical system, viz., the central, the infrabasals, the

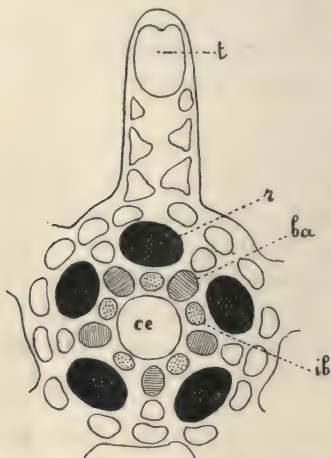


FIG. 84.—Apical system of a young Ophiurid *Amphiuroid squamata* (after P. H. Carpenter). *ba* basal; *ce* central; *ib* infrabasal; *r* radial; *t* terminal.

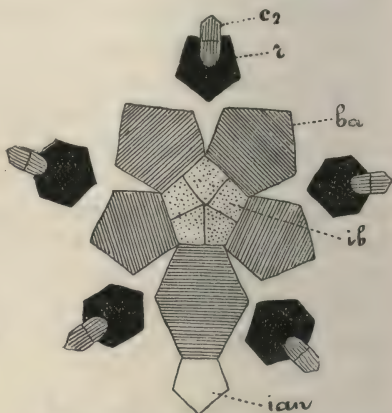


FIG. 85.—Apical system of a Crinoid (*Cyathocrinus*). *ba* basal; *c2* second costal (primibrach); *ib* infrabasal; *ian* anal interradial; *r* radial (from Lang).

basals and the radials are developed round the right coelomic vesicle of the larva, the terminals are five radially placed plates on the oral wall of the left coelomic sac. They become the oculars of Echinoids and those plates of Asteroids and Ophiuroids which are placed at the ends of the arms on the aboral side of the projecting end of the radial water-vascular canal.

The question as to whether these plates are in all cases homologous is a very difficult one to answer. It was originally suggested by Lovén and has been maintained by many of the later students of the group—notably by P. H. Carpenter—that there is a general homology between these plates in the different classes; but recently some doubt has been thrown upon this view of them (see p. 292). It is possible

that the very remarkable similarity in their arrangement may be due to the similarity in the general structural conditions, viz. the presence of a central point round which the plates are regularly arranged. This view derives some support from a consideration of the fact that when the matter is minutely examined there is a considerable amount of variation in the arrangement of the apical plates. For instance the apical pole may be occupied by a central plate (many Echinoids, larva of *Antedon*, many Asteroids and Ophiuroids), or by five interradially placed plates (basals in many irregular Echinoids), or by five radially placed plates (infrabasals of some Crinoids). Again the number of circles of these plates varies considerably. In many Crinoids there are three, viz. infrabasals, basals, radials. The same arrangement occurs in many Asteroids and Ophiuroids, but in these classes there is the greatest variation in the arrangement of the plates near the apical pole, and in many of them the plates in this region are small and numerous and the typical apical plates cannot be recognized. In Echinoids, on the other hand, there is never more than one circle, the interradially placed basals.

The **alimentary canal**. The variations in the position of the mouth and anus have already been indicated (p. 117). The alimentary canal passes between the two, and is chiefly remarkable for the very general absence of separate glandular appendages. The anus is absent in the adult of Ophiuroids and of a few Asteroids. For details the reader is referred to the account of the different classes.

The **central nervous system** consists of three parts which are variously developed in the different classes. (1) The ventral, (2) the deep oral, (3) the apical.

The **ventral** system consists of a concentration of a diffuse subepithelial plexus, found in most parts of the body in both ectoderm and endoderm. It is mainly a sensory system and supplies the skin, the feet and the gut. The ectodermal part of this plexus, which is continuous with the endodermal and may be called the **ectoneural**, is especially concentrated in an annular tract round the mouth (circumoral nerve ring) and in prolongations of this along the whole length of the radii (radial or ambulacral nerves). These concentrations constitute what we have called the **ambulacral central nervous system**.

The general disposition of the ectoneural plexus is well shown in Fig. 86: it extends into the tube-feet, in some of which, especially in the pointed variety, it is well developed, as well as into the spines, papulae and pedicellariae. The endodermal part of this plexus, which is called the **endoneural** and presents in Asteroids special concentrations round the edge of the mouth

opening (perioesophageal nerve ring), is found throughout the endoderm and is apparently continuous at the mouth and possibly at the anus with the ectoneural plexus.

In Echinoids, Holothurians and Ophiuroids, the circumoral ring and radial nerve trunks are separate from the superficial ectoderm and placed in the wall of a canal, the **epineural canal** (Figs. 140, 169, 180), which is actually formed in development by the invagination of the larval ectoderm along the centre of each radius * (p. 150). So that in these forms the ectodermal part of the central nervous system attains its internal position by invagination as it does in Enteropneusta and Verte-

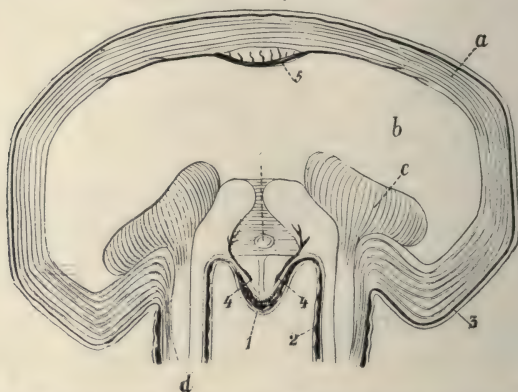


FIG. 86.—Scheme of the nervous system of the arm of a starfish (after Cuénot). *a* wall; *b* body-cavity of arm; *c* ampulla of tube foot; *d* tube foot; *e* radial canal of water-vascular system; 1 radial portion of ectoneural central nervous system; 2 ectoneural plexus of tube-foot; 3 ectoneural plexus of skin; 4 Lange's nerve cords (deep oral); 5 mesoneural plexus just beneath the longitudinal muscle.

brata, and the epineural canal may be compared to the central canal of the nervous system of those animals. Special nerve trunks pass from the central parts of this system to the skin, tube-feet, etc. At the end of the radii these radial trunks pass to the surface and lie in the ectoderm covering the terminal tentacle, if such is present. In the same three classes the apical nervous system (see below) is not present, or at any rate not developed in the same marked manner that it is in Crinoids and Asteroids.

The **deep oral nervous system** consists of a double cord in each

* This has been shown for Echinoids by MacBride, for Ophiuroids by Grave, and for Holothurians by Clark.

radius just within the radial nerve thickening of the ectoneural system, being only separated from the latter by a thin layer of connective tissue (Fig. 86, 4). These are called Lange's cords after their discoverer. They lie in the outer wall of the perihæmal canal and are mesodermal in origin. They are said to be exclusively motor in function. Round the mouth there appears to be a more or less complete ring belonging to this system in Asteroids and Ophiuroids, but this is absent or much less developed in Echinoids and Holothurians. The deep oral system is not present in Crinoids, or, if it is present, it lies deep on each side of the water-vascular canal (Fig. 197).

The **apical nervous system** is also mesodermal and motor. It has the form of a cord in the dorsal middle line and is developed from the dorsal peritoneum with which it sometimes remains continuous (Asteroids, Fig. 86). It is best developed in Crinoids (p. 283), where it is separate from the peritoneum; it is not found in Holothurians.

The **sense organs**, so far as they are understood, are mainly of a tactile nature. There are the tube-feet, which are all highly sensitive, and in some cases (Crinoids, Ophiuroids, certain tube-feet of Echinoids and Holothurians) exclusively concerned with sensation (and respiration). There is the unpaired tentacle, formed by the projecting end of the radial water-vascular trunk, at the end of the radii; in the early larvae this is the only tentacular or tube-foot structure present. Lastly there are the circumoral tentacles of Holothurians, which contain prolongations of the water-vascular system and are used for grasping, and the buccal tube-feet of regular Echinoids. In some Crinoids there are special tube-feet near the mouth which may be regarded as circumoral tentacles. The circumoral tufts of Echinoids are respiratory in function and not connected with the water-vascular system.

Of other tactile structures we must mention the spines which are richly provided with nervous tissue.

Special organs of sense are not numerous. The pigment spots at the end of the arms of Asteroids are probably visual in function (p. 175), as are also the shining spots on the skin of *Diadema* (an Echinoid, p. 230). The ocular plates of Echini have no visual structures on them and are merely perforated by the terminal tentacle of the water-vascular canal.

Otocyts are found in Holothurians (Synaptidae and Elasiopoda), in connexion with the radial nerves (p. 256).

Finally the **sphaeridia** of Echinoids (p. 227) are probably organs of some special sense. They are modified spines, and are richly provided with nervous tissue. It has been suggested that they are organs of orientation, enabling their possessor to perceive its position in space.

The **muscular system** is very variously developed in the different classes. In Holothurians, only, is there a well-marked dermo-muscular body-wall. In all other Echinoderms the skin is not contractile or but slightly contractile, and the muscles are restricted to special bands acting on particular skeletal plates or other part of the body, and to the muscular elements in the walls of the tube-feet and water-vascular system generally and of the viscera. In the spiniferous forms there are special muscles attached to the base of the spines and pedicellariae.

The muscular tissue consists of smooth contractile fibres without transverse striation, except in the case of the muscles of some of the pedicellariae and of a few spines.

The Coelom. Our knowledge of the coelom of Echinodermata has been of slow growth. It began with the discovery of A. Agassiz * that the enteron of the larva of *Asterias berylinus* gave rise not only to the alimentary canal of the adult, but also to the body-cavity and water-vascular system. This discovery was established and extended by the work of Metschnikoff on Asteroids, Echinoids, and Ophiuroids, of Kowalevsky and Selenka on Holothurians, of Bury on Crinoids, and of Ludwig on Asteroids. Finally the recent work of MacBride has not only elucidated the relations of the genital organs and of the so-called periaermal spaces, but has thrown light upon the nature of that organ which was formerly called the "heart" but is now more commonly referred to as the axial organ or ovoid gland.

The coelom arises from the enteron of the embryo as a single pouch. This pouch soon separates from the enteron and divides into a number of sacs, one or one pair of which constitutes the **hydrocoel**, the others the **splanchnocoel**. The left hydrocoel† gives rise to the water-vascular system, while the splanchnocoel

* "Embryology of the Starfish," *Contributions to the Natural History of the United States*, 5, 1864.

† The right hydrocoel, when present, is always very small, and takes no part in forming the water-vascular system.

becomes transformed into the perivisceral cavity and its associated spaces (axial sinus, aboral sinus, perihæmal canals) of the adult.

All the coelomic spaces are lined by an epithelium, which in the case of the water-vascular system and perivisceral cavity is ciliated, and they all contain an albuminous fluid in which amoeboid cells float.

Nothing of the nature of **nephridia** is known in the group, but one of the divisions of the splanchnocoelic part of the coelom, viz. that known in the larva as the anterior coelom, has an opening to the exterior. This opening is called the **primary water pore** or the **madreporitic pore**. The primary water-pore, which is frequently in special relation with a dermal plate called the **madreporite**, and is always interradial in position, may be a small simple opening or it may be subdivided (Asteroids, Echinoids, many Ophiuroids) into a large number of minute secondary pores, which are more or less closely aggregated together on the madreporite. Though the generative organs are separate from the coelom in the adult, the primitive germ cells which give rise to them have a coelomic origin.

We may now proceed to consider the different parts of the coelom in greater detail, and first of all we will treat of the spaces derived from its splanchnocoelic division. These are three in number: the perivisceral cavity, the axial sinus and the perihæmal spaces.

1. The **perivisceral cavity** or body cavity proper is always well developed and in relation with the alimentary canal and principal viscera. It is developed from the right and left posterior coeloms of the larva and it never communicates with the exterior except in Crinoids in which the water-pores open into it (see p. 287). It is often traversed by complete or incomplete mesenteries (Holothurians) or by strands of connective tissue, which pass from the body wall to the wall of the alimentary canal. In the brachiopods the arms always contain prolongations of the perivisceral cavity. As stated above, it usually has a ciliated lining and contains an albuminous corpusculated fluid.

The **Amoebocytes** of the coelomic fluids and possibly of other organs play an important part, as was first shown by Durham (*op. cit.*), in removing foreign bodies from the organism. They act as phagocytes and pass to the exterior by diapedesis through the walls of the papulae on the outside of which they disintegrate.

Several kinds of amoebocytes,* differing in size, character of granulations and shape, are found in the coelomic fluids and tissues of the body. In some cases spherical cells provided with a long cilium have been observed (e.g. coelomic fluid of *Dorocidaris*). In *Echinus* the amoeboid cells have been observed to unite and give rise to plasmodia and networks.† In the larva they play an active part in the absorption of the calcareous skeleton, and in both larva and adult isolated amoeboid cells take part in tissue formation.

2. The **axial sinus** is distinct from the perivisceral cavity in all classes except in the adults of Crinoids and some Holothurians (see pp. 129, 152). It is developed from the anterior coelom of the larva and communicates with the exterior by the water-pore or pores, and the stone-canal opens into it. It will be convenient to reserve what we have to say about the two latter structures until we have dealt with the water-vascular system.

In Asteroids the axial sinus (i.e. the space into which the stone-canal and axial organ project) is continued ventrally round the mouth and forms the so-called *inner circumoral periaemal space* (Fig. 131). This space is not connected with and must not be confused with the periaemal space about to be described.

3. The **periaemal spaces** (sinus system) usually consist of an annular circumoral space which is called the outer in contradistinction to that just mentioned, and of five tubes placed along the radii between the radial nerve cord and the radial water-vascular trunk (Fig. 131). This system of spaces appears to be unrepresented in Crinoids. It is lined by an epithelium and has been definitely traced in Asteroids to outgrowths of the posterior and anterior body-cavities of the larva (p. 145). The periaemal system must not be confused with the epineural canal of Ophiuroids, Echinoids, and Holothurians (p. 124), which lies superficial to the radial nerve cord and has an epithelial lining which must be regarded as ectodermal.

The *aboral circular sinus* (Fig. 131) might be included amongst the periaemal spaces; it is a development of the left posterior coelom and is in relation with the generative rachis (see p. 146).

The **water-vascular system** is derived from the left hydrocoel (p. 144). It is very similarly developed in all classes of Echinoderms. It is the organ which pre-eminently displays the radial structure of the body, and is the first to show it in the larva. It consists of a circular vessel round the mouth with as many

* Cuénot, *Arch. Zool. Exp.* (2), 9, 1891, p. 613.

† Théel, *Festschrift Lilljeborg Upsala*, 1896, 3, p. 47

tubular prolongations as there are radii. These are the radial water-vascular vessels; they give off lateral branches to the tube-feet all along their course (Fig. 133).

The **tube-feet** are hollow, cylindrical or conical processes of the body wall, and the space within them is continuous with the water-vascular system by the just mentioned lateral branches of the radial vessels. At their inner ends they are connected with small vesicles—the **ampullae** (Fig. 129, 26). Ampullae are absent in Crinoids and Ophiuroids; they have muscular walls and their function is to drive the fluid into the tube-foot and so to cause its extension. The retraction of the foot is brought about by the contraction of the muscles in its wall, the fluid in the tube-foot passing into the ampulla.* In the forms with ampullae the tube-feet are locomotive and adhesive organs. Their free ends terminate in sucker-like discs which adhere to foreign bodies. When ampullae are absent (Crinoids and Ophiuroids) the tube-feet are purely sensory and respiratory in function and cannot be used for adhesion and locomotion. Calcareous bodies are often present in the connective tissue layer of the tube-feet, particularly at the sucker-like termination.

The circumoral vessel frequently possesses accessory structures opening into it in its interradiial portions; these are the bladder-like **polian vesicles** (p. 184) and the gland-like **Tiedemann's bodies** (p. 185).

The water-vascular system is indirectly connected with the exterior by a canal called the **stone- or sand- canal** (Figs. 133, 136). The stone-canal owes its name to the fact that it frequently contains in its walls a large amount of calcareous matter, which readily breaks through the lining and falls into the canal, where it is found as gritty matter. The connexion with the exterior is effected in the following way (Fig. 132): the stone-canal passes off from the circumoral vessel in one of its interradii to open, in the larva, into the anterior coelom which is a portion of the splanchnocoel. The anterior coelom, which, as already explained (p. 127), opens to the exterior by the water-pore, persists into the adult in Asteroids, Ophiuroids, and Echinoids as a distinct space, the axial sinus.† In Crinoids it is a distinct space in the

* For the valve assisting in this process, see p. 182.

† In the adult many of the pores of the madreporite come to open directly into the dorsal end of the stone-canal, but the opening of the stone-canal into the axial sinus is always maintained.

young larva, but later becomes merged in the general perivisceral cavity, so that in the adult both the stone-canals and the water pores open into the perivisceral cavity. In Holothurians the anterior coelom is very feebly developed, but as Bury has shown it can be traced through the whole development (p. 152) and has the appearance of a small appendage of the stone-canal (Fig. 108). In a few Holothurians it retains its communication (by the water-pore) with the exterior, but in the majority the water-pore closes in the adult, and the walls of the anterior body-cavity largely break down and give rise to the so-called internal madreporite. It thus comes about that in most Holothurians the stone-canal appears to open directly into the general body cavity.

It sometimes happens (some Asteroids and Ophiuroids, Crinoids) that there is more than one primary water-pore; in such cases there is a corresponding increase in the number of madreporites and stone-canals, and they are generally placed in different interradii. In Crinoids there are never less than five primary water-pores, and generally they are much more numerous. In the former case there is one water-pore and one stone-canal in each interradius; in the latter case there are many of both structures in all the interradii, and an exact correspondence between the stone-canals and water-pores, though it may exist, cannot be shown.

The water-vascular system is lined by a flat ciliated epithelium and contains an albuminous fluid with leucocytes very similar to that found in the perivisceral cavity and sinus system. Its function is mainly locomotory, but to this must be added, especially in forms in which the tube-feet are without ampullae, a tactile and respiratory function. By some authors it has been regarded as in part excretory, but there seems to be little evidence in support of this. There might be something to be said for this view, if the current through the madreporite set outward, but the reverse appears to be the case (Ludwig). If there is any current through the water-pore, it appears to be an inward one as a result of which sea-water is drawn into the system. But it may be that on occasion the direction of this current is reversed. Particles of carmine injected into the water-vascular system are taken up by the cells of Tiedemann's bodies (Kowalevsky).

The **axial organ**, which goes by various names, e.g. dorsal organ, ovoid gland, heart, etc., is found in Echinoids, Asteroids (Fig. 130), Ophiuroids and Crinoids. It is developed as a fold

of the wall of the axial sinus (except in Crinoids, p. 159), and consists of connective tissue and of cells which have grown into it from the genital rudiment of the larva. It is covered towards the axial sinus by the coelomic epithelium. Its walls are folded so that it appears to be penetrated by tubular prolongations of the epithelium of the axial sinus and of the perivisceral cavity. Some observers have attributed to the axial organ a lymphatic gland function, and have supposed that it buds out amoeboid cells into the axial sinus, but this is extremely doubtful. In Echinoids it takes up carmine injected into the body cavity (Kowalevsky). As stated above the primitive germ cells grow into it, so that it is connected in the adult with the generative rachis. The axial organ is absent in Holothurians.

Excretion. Very little is known about excretion in Echinoderms. There do not appear to be any special organs devoted to it. It is possible that there may be some organ in connexion with the water-vascular system or with the axial sinus which is concerned with the elimination of the nitrogenous waste, for these organs open to the exterior by the water-pore—but no such organs have been certainly identified.

The so-called **vascular system**, which is found in all classes and appears to be specially well developed in the Holothurians and Echinoids, is formed of a peculiarly modified connective tissue in which the fibres are sparse, and which contains intercommunicating spaces without an epithelial lining. The fluid in these spaces does not appear to undergo any definite movement. The real nature of this tissue is doubtful. By some observers it has been regarded as a lymphatic gland, a view which is suggested by the appearance, sometimes found, of amoeboid cells being budded off from it. Typically there is a circumoral tract of it with radial prolongations which lie between the radial water-vessel and the radial nerve cord; an annular aboral tract of it, in which the generative rachis is embedded and which sends extensions to the genital organs; and in Holothurians and Echinoids a considerable development of it in the mesentery and on the gut wall. An account of its occurrence will be found in the description of the different classes.

The **generative glands** * of Echinoderms are peculiar in the

* G. W. Field, on the Morphology and Physiology of the Echinoderm spermatozoa, *Journ. Morph.*, Boston, 2, 1895, p. 235.

fact that they open directly to the exterior and apparently have no relation to the coelom. The researches of MacBride have however shown us that the cells composing them are, in Asteroids, Echinoids and Ophiuroids, coelomic in origin, being derived from lining cells of the body-cavity, and this will probably be found to hold throughout the phylum. Another peculiarity of them consists in the fact that in all classes, with the possible exceptions of Holothurians (see below), they are connected with a cellular cord, disposed in different ways in the different classes and called the **generative rachis**. Indeed they may be regarded as swollen, fertile portions of this rachis, the rest of which is sterile and does not produce generative cells. As stated above the axial organ contains a prolongation of the generative rachis.

There are no accessory glands of any kind. The generative products when ripe are in nearly all cases discharged directly into the sea, where the ova are fertilized and undergo their development. In rare cases the eggs are retained in special brood pouches or on the skin of the mother. Secondary sexual characters are as a rule not developed.

The generative organs usually consist of tufts of branched tubes which open directly on the surface. In Crinoids they are contained in the pinnules as hollow structures without any opening to the exterior, and the manner of escape of the generative cells is not certainly known, but it probably takes place by dehiscence. In Asteroids, Ophiuroids, and Echinoids they are pentamerously arranged in the interradii and participate in the radial symmetry of the body; they open interradially and sometimes dorsally. In Holothurians, which are sometimes said to be without the generative rachis,* they are present as a single tuft of tubes which open in the adult-dorsal middle line.

The Echinoderms are exclusively marine animals.† They are found on the floor of the ocean from the littoral to the abyss. Very few pelagic forms are known. They are almost all slowly

* Holothurians possess a cord containing germ cells and passing from the point of union of the genital tubes along the generative duct towards the body wall (Théel, *Bih. Svenska Akad. Handl.*, 27, Afd. 4, No. 6, 1902). This is probably the generative rachis.

† *Synapta similis* inhabits brackish water of the mangrove swamps of Bohol (Ludwig).

creeping creatures, moving by means of their tube-feet or by their arms (Comatulids, Ophiuroids). Most Crinoids however are attached by a stalk which is a prolongation of the aboral surface of the body, but they may become detached and acquire a new attachment (*Pentacrinus*).

From a psychical or nervous point of view, the Echinoderms are extremely low in the scale of life, but judging them from the complexity of their organization apart from the nervous system, they approximate to the so-called higher animals. Geologically they are of great interest, the structure of the body wall lending itself very readily to their preservation as fossils. They make their appearance in the Cambrian and in the Silurian with a range of structure not unlike that which characterizes living forms.

The power of regenerating lost parts is considerable in almost all Echinoderms, and many of them, especially those with long arms, possess the power of autotomy. It is least developed in Echinoids, but in Asteroids and Ophiuroids it is in some cases so extensive that not only may arms and portions of the disc be regenerated, but the whole body may be reformed from a single arm. In Crinoids and Holothurians the viscera even are capable of regeneration.

Asexual reproduction is found in many Asteroids, Ophiuroids and Holothurians. It takes the form of fission into two equal halves, in the two former classes the plane of fission passing through the disc, in the latter transversely to the long axis of the body.

In this work the Echinodermata are divided into seven classes: Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea, Crinoidea, Cystidea, Blastoidea. The mutual relationships of these are discussed under the accounts of each class. The group Pelmatozoa is considered and the reasons for not adopting it are stated on p. 303 et seq.

Development.* In the great majority of Echinoderms the

* For a more complete account of the development of the *Echinodermata*, the reader is referred to the following works, where the older literature will be found: F. M. Balfour, *A Treatise on Comparative Embryology*, vol. 1, London, 1885. E. Korschelt and K. Heider, *Textbook of the Embryology of Invertebrates*, English Translation, London, 1895. A. Lang, *Text-Book of Comparative Anatomy*, English Translation, vol. 2, London, 1896. Of recent workers the following may be cited: E. W. MacBride, The development of *Asterina gibbosa*, *Q.J.M.S.*, 38, 1896, p.

egg is small and the entire development takes place in the sea, and in most of them there is a free-swimming, externally bisymmetrical larval stage. In about fifty species however the young remain in connexion with the mother during their development and care of the brood occurs, and in some cases (e.g. *Asterina gibbosa*) a free-swimming larva is not formed. In such cases the egg is usually larger than when a free-swimming larva is formed, owing to the presence of a greater quantity of food-yolk.* When care of the brood occurs,† the young may either creep about freely on the surface of the mother, or they may be attached to special parts of the body wall, e.g. the neighbourhood of the mouth, among the spines of the back, in special depres-

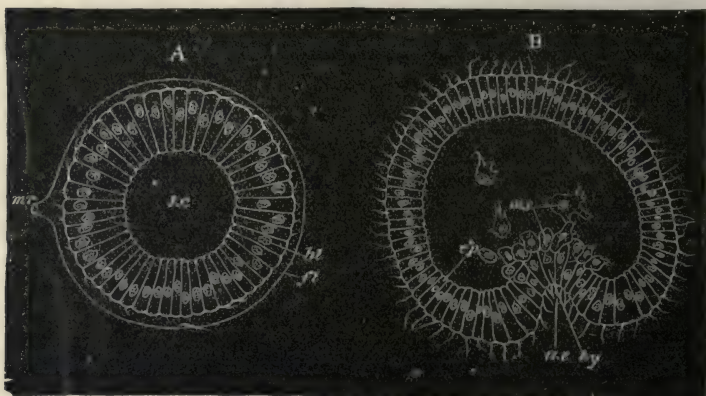


FIG. 87.—Two stages in the development of *Holothuria tubulosa* viewed in optical section (from Balfour, after Selenka). A, Blastosphere at the close of segmentation. B, commencing gastrula stage. *ae* archenteron; *bl* wall of blastosphere; *ep* ectoderm; *fl* vitelline membrane; *hy* endoderm; *mr* micropyle; *ms* protoplasmic immigration into the segmentation cavity from the invaginating endoderm; *sc* segmentation cavity.

sions of the skin. In some Holothurians the development takes place in the body cavity, and in the dioecious *Chiridota contorta* in the genital tubes. In the starfish *Stichaster nutrix* the young

339. Id., The development of *Echinus esculentus*, *Phil. Trans.*, 195, 1903, p. 285. H. Bury, The Metamorphosis of Echinoderms, *Q.J.M.S.*, 38, 1895. H. Théel, The development of *Echinocyamus pusillus*, *Nova Acta R. Soc. Sci. Upsala*, 1892. Id. Prelim. Account of the development of *Echinus miliaris*, *Proc. Roy. Swedish Acad.*, 28, 1902. G. W. Field, The larva of *Asterias vulgaris*, *Q.J.M.S.*, 34, 1893, p. 105. S. Goto, The metamorphosis of *Asterias pallida*, etc., *Journal Coll. Sci. Imp. Univ., Tokyo*, 10, 1898, p. 239. Id., Metamorphosis of *Asterina gibbosa*, *Ibid.*, 12, 1898, p. 227. Th. Mortensen, Echinoderm-larven, *Ergeb. d. Plankton-Exped. d. Humboldt-Stiftung*, 2, 1898.

* In *Benthodytes sanguinolenta* the eggs measure 2 mm. in diameter.

† Ludwig, *Zoolog. Jahrb.*, Suppl. Bd., 7, 1904, p. 683.

undergo their early development in the stomach of the mother. Care of the brood is found most frequently in forms inhabiting the colder seas.

With a few exceptions the early development, so far as it is at present known, may be summarized as follows. The egg is fertilized in the sea, undergoes a total cleavage, and becomes transformed into a hollow one-layered blastosphere. At one pole of the blastosphere an invagination makes its appearance and a typical gastrula is formed (Fig. 87). The invaginated cells constitute the endoderm, the cavity bounded by them the archenteron, and the opening of the archenteron the blastopore.

The archenteron rarely if ever fills the segmentation cavity, but the latter soon becomes traversed by a nucleated protoplasmic network (Fig. 88), which is continuous both with the endoderm and with the ectoderm (outer cells of the gastrula), and constitutes the first trace of the mesoderm. This meso-

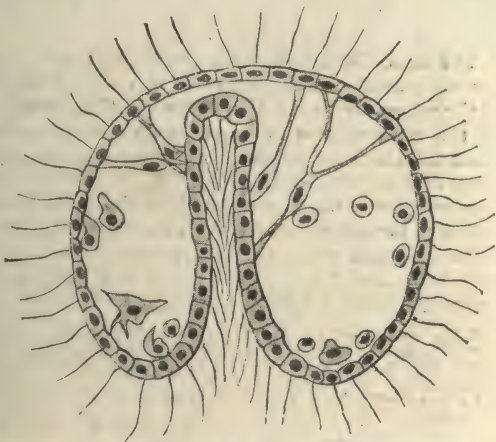


FIG. 88.—Gastrula stage of *Toxopneustes brevispinosus* (from Korschelt and Heider, after Selenka). The mesodermal network (so-called mesenchyme) is shown traversing the blastocoel and continuous with both ectoderm and endoderm.

dermal network, which is reinforced from the later appearing enterocoelic vesicles is commonly called **mesenchyme** and gives rise to the connective tissues, to some of the muscles, and to the calcareous structures of the body.

Different views may be held as to the origin and structure of this early appearing mesodermal network. The usual view is that it consists of amoeboid cells which arise by the proliferation of the epithelial cells of the embryo in the blastosphere and later stages, and wander into the blastocoel. Another view for which there is much to be said is that the blastocoel at its very first appearance is traversed by protoplasmic processes of its walls,* and that the apparent proliferation of cells of the

* See C. Shearer on the connexions between the blastomeres of embryos in the *Proc. Roy. Soc.*, 1906.

endodermal pole of the blastosphere or of the invaginating endoderm, etc., is really only a proliferation of nuclei, and that the migration of cells into the blastocoel is nothing more than the shifting of these nuclei along the strands of the protoplasmic reticulum which has traversed the blastocoel from its first appearance. On this view the embryo must be regarded not as an aggregation of separate cells, but as a continuous structure with different densities of protoplasm in different parts. Thus in the blastosphere stage the bulk of the protoplasm is concentrated in a peripheral layer to which the nuclei are confined, the central portion being occupied by a sparse non-nucleated reticulum. As to the meaning of this peculiar peripheral aggregation of the protoplasm and nuclei, which is characteristic of the blastosphere of so many pelagically developing animals, we are quite in ignorance. It has been suggested that it represents some ancestral stage of structure common to all the organisms in which it occurs. On the other hand it may be argued, perhaps with greater force, that the condition is due to some physiological necessity, possibly of a nutritive nature, which is felt by all organisms developing in the open sea.

The undoubted fact of the presence of free leucocytes in the fluids of the body must not be held to be at variance with the view of the nature of the mesenchyme mentioned above. The view of the essential continuity of the mesenchyme is based upon Comparative Embryology. In all cases in which its structure has been thoroughly made out, it has the form of a network continuous both with ectoderm and endoderm. The free leucocytes which are found in the body fluids are products of this network, formed no doubt for a definite purpose. What that purpose is has been largely explained by the remarkable and penetrating observations of Metschnikoff,* though the causes which govern the budding off of the leucocytes have not been ascertained.

The eggs when laid are enclosed in the vitelline membrane (Fig. 87), but they soon acquire a coat of cilia and become free. The gastrula has a somewhat oval form with the blastopore at one end and one surface slightly flattened. The end carrying the blastopore is posterior and the flattened surface is ventral. The archenteron now bends towards the ventral surface anteriorly, where, its wall having fused with the ectoderm, it acquires an opening to the exterior; this is the larval mouth, the posterior opening or blastopore persisting as the larval anus (except in Crinoids).

The fate of the larval mouth and anus varies in the different classes. In Holothuroidea they usually persist into the adult. In Ophiuroidea the larval mouth persists but the anus closes, the adult being without one. In Asteroidea and Echinoidea the larval mouth and anus close and the oesophagus atrophies, the adult mouth, oesophagus, and anus being new formations. It is possible, however, that in some Asteroidea they may persist. In Crinoidea there is no larval mouth or anus, and the blastopore closes at an early stage.

* See the numerous papers by this author dealing with the importance of the amoeboid cells in the organism and especially his great work on *Immunity*, English Translation, Cambridge, 1905.

Later the anus shifts on to the ventral surface, and the cilia become confined to definite tracts or bands. According to the arrangement of these ciliated bands, two main types of larvae can be distinguished. In one (*A*, Fig. 89) there is a single longitudinal band of cilia which passes across the ventral surface immediately in front of the mouth and in front of the anus, and bounds a depression on the ventral surface into which the mouth opens. This is the **Auricularia** type of larva which is found in Holothurians; a modification of it is found in Echinoids and Ophiuroids, where it is known as the **Pluteus** larva (Fig. 94). In the other (*B*, Fig. 89) there are two bands of cilia, the one preoral and encircling the preoral lobe, the other longitudinal in appearance, but really postoral, forming a complete circuit of the body between the mouth and the anus; this is the **Bipinnaria** type of larva and is characteristic of Asteroids. The larvae of both these types are externally bilaterally symmetrical and have been so since the ventral surface became distinct. They remain symmetrical externally for some time longer, but at about this stage, or in some cases even

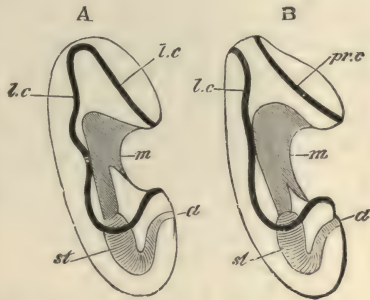


FIG. 89.—*A*, the larva of a Holothurian (Auricularia type); *B* of an Asteroid (Bipinnaria type), both seen from the left side (from Balfour). *a* anus; *m* mouth; *st* stomach; *l.c.* longitudinal ciliated band; *pr.c.* preoral ciliated band.

before this stage is reached, their internal structure begins to show traces of that asymmetry which is so characteristic of the later larvae and eventually leads to the establishment of the radial symmetry of the adult. Before, however, considering

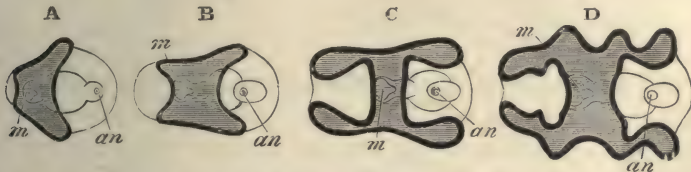


FIG. 90.—A series of diagrams representing the evolution of an auricularia larva from the simplest Echinoderm larval form, ventral view (from Balfour). The black line represents the ciliated band. The shaded part is the oral side of the ring (oral depression, see Fig. 89), the clear part the aboral side of the larva. *m* mouth; *an* anus.

before this stage is reached, their internal structure begins to show traces of that asymmetry which is so characteristic of the later larvae and eventually leads to the establishment of the radial symmetry of the adult. Before, however, considering

these internal changes it will be well to consider briefly the various forms which the bilateral larva may assume.

The auricularia larva. In the Holothurians the ciliated band becomes elongated and sinuous, as is shown in the series of diagrams in Fig. 90. A completely developed *auricularia* larva of a Holothurian is shown in Fig. 91. The sides of the body are prolonged into processes which correspond to the arms of the bipinnaria and pluteus, and there is a well-marked preoral lobe. Calcareous structures in the form of spheres, wheels and star-shaped bodies are formed, but there are no calcareous rods. In some species (*Auricularia stelligera* and *sphaerigera*) peculiar elastic spheres, the nature of which is not known, are present.

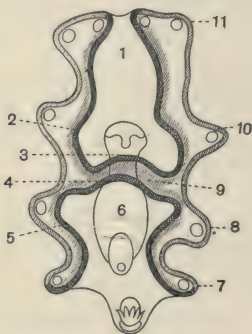


FIG. 91.—*Auricularia stelligera*, ventral view (after J. Müller). 1 frontal area; 2 preoral process; 3 anterior, 4 posterior portion of the ciliated band; 5 postoral process; 6 anal area; 7 postero-lateral process; 8 postero-dorsal process; 9 oral depression; 10 dorso-median process; 11 antero-dorsal process.

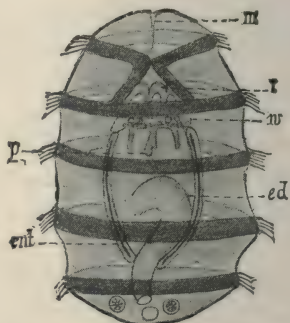


FIG. 92.—Pupal stage of the larva of *Synapta digitata* (from Korschelt and Heider, after Semon). *ed* hind-gut; *ent* right body-cavity; *m* oral funnel; *w* water-vascular ring, with out-growths into tentacles *t* and radial vessels *p*.

The larva now enters the so-called pupa-stage, in which it has the form of a barrel with five ciliated hoop-like bands (Fig. 92). The pupa is formed from the *auricularia* in the following way:—The ciliated ring breaks up (Fig. 93) into pieces which rearrange themselves into the five rings of the pupa and the oral ring; the mouth and surrounding parts, including the oral ring, retreat into the interior, giving rise to the oral vestibule (atrial cavity), the opening of which narrows and passes to the left side. Eventually the atrial opening becomes terminal by the atrophy of the small preoral lobe, and the epithelium of the oral ring

becomes the epithelial covering of the tentacles which at first project into the atrial cavity. When the adult condition is

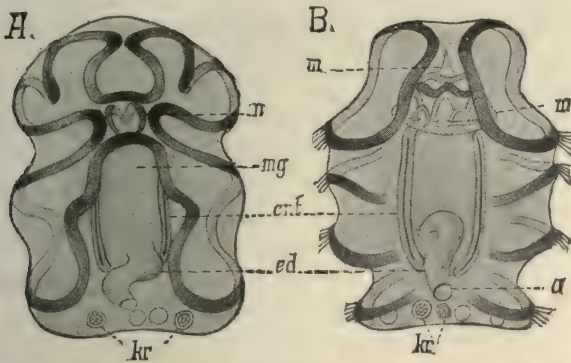


FIG. 93.—*Synapta* larva, showing the break up of the ciliary band of the auricularia. *a* anus; *ed* proctodaeum; *ent* enterocoel; *kr* calcareous wheels; *m* oral funnel or atrium; *mg* stomach; *n* nerve bands; *w* water-vascular ring with prolongations (from Korschelt and Heider).

attained the ciliated bands disappear, the oral vestibule opens out and the tentacles project.

The pluteus larva. In the Ophiuroidea and Echinoidea the larva resembles the auricularia in possessing a single ciliated band, but differs from it by the long arm-like processes of the

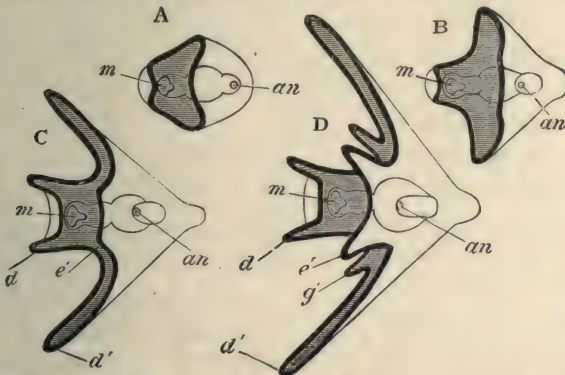


FIG. 94.—Diagrammatic figures showing the evolution of an ophiuroid pluteus from a simple Echinoderm larva (from Balfour, after J. Müller). The calcareous skeleton is not represented. *m* mouth; *an* anus; *d* antero-lateral arms; *d'* the long postero-lateral arms; *e'* postoral arms; *g'* postero-dorsal arms.

margin of the body on to which the ciliated band is continued, by the small size of the preoral lobe (frontal area) and by the

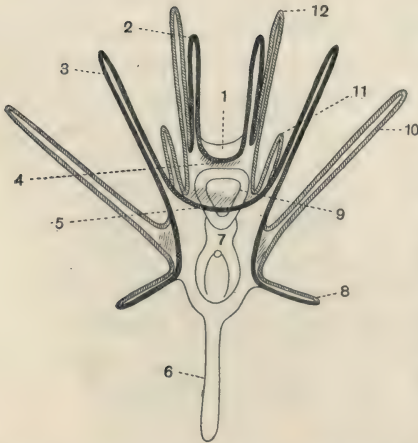


FIG. 95.—Echinopluteus of a Spatangid (after J. Müller). 1 frontal area; 2 preoral arm; 3 postoral arm; 4 anterior; 5 posterior transverse portion of ciliated band; 6 unpaired posterior arm; 7 anal area; 8 postero-lateral arm; 9 oral area; 10 postero-dorsal arm; 11 antero-dorsal arm; 12 antero-lateral arm.

wards or outwards, preoral arms are present, and in Spatangid larvae (Fig. 95) there is an unpaired posterior arm on to which the ciliated band is not continued. Moreover in some genera (*Echinus*, *Strongylocentrotus*, *Sphaerechinus*) there are in old larvae four ciliated projections, called *ciliated epanlettes* (Fig. 96), at the base of the postoral and postero-dorsal arms, and sometimes an additional pair at the hind end of the body. *Ciliated lobes* (auricular appendages, auricles) are cutaneous expansions between some of the arms in certain echinoplutei, and pedicellariae may appear before the larval characters are lost. In ophioplutei the calcareous skeleton is in two halves, each

great development of the postanal part of the body (Fig. 94). The arms are supported by calcareous rods.

The plutei of Ophiuroids and Echinoids are distinguished as *ophio-plutei* and *echinoplutei* respectively. In ophioplutei the postero-lateral arms are always the largest and directed forwards (Fig. 94), and preoral and antero-dorsal arms are absent. In echinoplutei (Fig. 95) the postero-lateral arms when present are directed back-

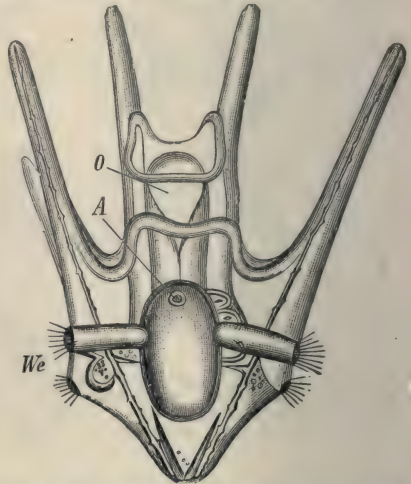


FIG. 96.—Pluteus larva of *Echinus lividus* with four ciliated epanlettes *We* (after Metschnikoff) from the ventral side. *O* mouth; *A* anus.

half proceeding from one calcification centre; in echinoplutei the skeleton arises from five or six centres.

The **bipinnaria larva**, found only in the Asteroidea, has two ciliated rings, one preoral and the other longitudinal and postoral (p. 137 and Fig. 89 B). In possessing a well-marked preoral lobe it resembles the auricularia, and its two ciliated rings must be regarded as having been derived by the division of the single band of the auricularia, a view which is supported by the fact that in some species (e.g. *Asterias rubens*, *A. glacialis*, *Astropecten*) they are at first connected dorsally. Further, Driesch* has shown that in some artificially reared bipinnariae there is only one band.

As in the pluteus a series of arms is formed along the lines of the two ciliated bands, and sometimes three arms, not connected with the bands and covered with warts, are formed in front of the preoral arms at the anterior end of the frontal area; these are the brachiolar arms and the larva bearing them the **Brachiolaria larva**.† The arms are without calcareous rods.

The median brachiolar arm replaces the ventral median arm and bears at its base a sucker ‡ by which the larva attaches itself during the metamorphosis. The ciliated band appears, as a rule, not to pass on to these arms (except in *Bipinnaria papillata*).

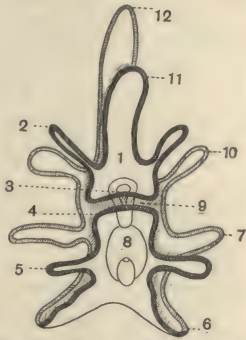


FIG. 97.—*Bipinnaria elegans*. 1 frontal area; 2 preoral arm; 3 anterior, 4 posterior transverse portion of the ciliated band; 5 postoral, 6 postero-lateral, 7 postero-dorsal arm; 8 anal area; 9 oral depression; 10 antero-dorsal, 11 ventro-median, 12 dorso-median arm (after Mortensen).

In the bipinnaria (and brachiolaria) the frontal area is well developed and surrounded by the preoral ring of cilia. There is a median ventral anterior arm and a median dorsal anterior (Fig. 97), neither of which is present in the auricularia or in the

* *Arch. f. Entwicklungsmechanik*, 20, 1906, p. 13.

† It is possible that the brachiolar arms, which serve for temporary attachment, are present in a later stage of all bipinnariae, for in the only two cases in which the life-history is fully known (*Asterias glacialis*, *A. vulgaris*) they are formed.

‡ It is probable that in all bipinnariae this disc, which serves for fixation during the metamorphosis, is present at a later stage in all cases, for not only is it present in the two cases mentioned in the last note, but it occurs in all cases thus far examined where a shortened development due to food yolk has brought these stages within range of easy observation (Ludwig, *op. cit.* p. 134). (Cf. *Anasterias*, *Asterias antarctica*, *Asterina gibbosa*, *Cribrella sanguinolenta*.)

pluteus. Antero-lateral arms are never present. The arms have muscles and are contractile, a fact which renders it difficult to preserve these larvae without distortion.

These are the principal types of larvae of the Echinodermata, but we must not omit to mention the vermiform Ophiurid larvae which are pelagic and the vermiform larvae of those Asteroids in which care of the brood occurs. The larva of *Asterina gibbosa* may be classed with the latter. Echinoderm larvae are found principally near the coast and in small waters: they are not characteristic of the plankton of the high seas. Only a few of the larvae are taken in more than one locality.

In the nomenclature of Echinoderm larvae when the adult is not known, the name of the kind of larva is used as that of the genus and a specific name is added. In this sense there are four genera of larvae, viz. *Auricularia* (confining this term to Holothurian larvae), *Ophiopluteus*, *Echinopluteus*, and *Bipinnaria* (including brachiolaria). When the adult is known specific names are not required.

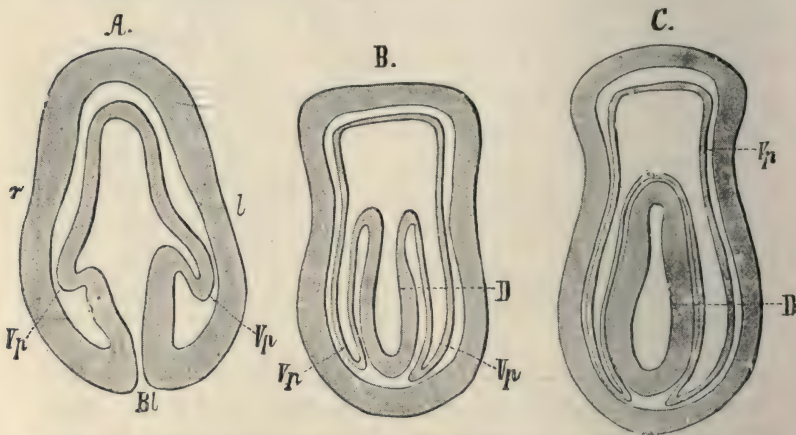


FIG. 98.—Longitudinal-horizontal sections through three successive stages of the larva of *Asterina gibbosa* (from Korschelt and Heider, after Ludwig). *A*, showing the first origin of the enterocoel *Vp* from the enteron; *B*, a later stage, the enterocoel is still in communication with the enteron *D*; *C* enterocoel cut off from the enteron and consisting of a median unpaired portion in front—the anterior body cavity, and two paired portions behind, the right and left posterior body cavities. *Bl* blastopore; *D* intestine; *Vp* enterocoel (vasoperitoneal vesicle); *r* and *l* right and left side of the larva. The hydrocoel has not yet made its appearance.

Development of internal organs and the metamorphosis. The coelom arises soon after the establishment of the gastrula as a single evagination of the enteron* (Figs. 98, 99). This soon separates from the enteron, and becomes divided into a number

* The term **vaso-peritoneal** is sometimes applied to the enteric pouch

of sacs, one* of which is called the **hydrocoel** because it gives rise to the water-vascular system and its lining; the others constituting the **splanchnocoel**, because they give rise to the body-cavity and its associated spaces of the adult. The mode of division is very similar throughout the group except in Crinoids, and is described below.

In Asteroids we may take as type *Asterina gibbosa* in which the development has been so fully worked out by Ludwig and later by MacBride. The eggs which are 0.5 mm. in diameter

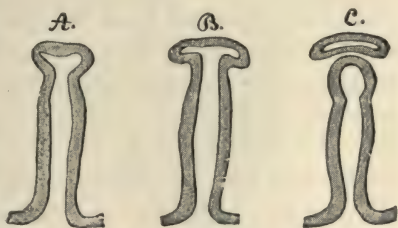


FIG. 99.—Longitudinal section of three stages in the formation of the enterocoel of *Echinus miliaris* (from Korschelt and Heider).

are attached to stones to which they adhere by means of the vitelline membrane. On about the fourth day the embryo ruptures the vitelline membrane and escapes. It is then found to possess a large preoral lobe (Fig. 100) the edge of which is thickened, constituting the larval organ. The larval organ surrounds a central depression and is covered with specially long cilia, by means of which the larva can swim. Later, in the centre of the concavity of the larval organ, a small elevation is formed. The ectoderm of this contains gland-cells which secrete an adhesive substance by means of which the larva

fixes itself during the metamorphosis. The temporary fixation which is possible during larval life appears to be due to a kind of cupping action brought about by the application of the preoral lobe to the substratum and the retraction of its central portion.

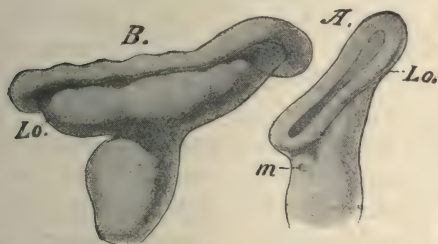


FIG. 100.—Larvae of *Asterina gibbosa* (after Ludwig). A, a younger stage, oblique ventral view. B, older stage from the side. Lo larval organ; m larval mouth.

and to the sacs which arise from it, the word enterocoel being retained for the peritoneal or body-cavity portions of the latter. We, however, prefer to call the totality of sacs **enterocoelic**, distinguishing the water-vascular portion as **hydrocoel** and the perivisceral portion as **splanchnocoel**.

* Or one pair (see footnote on p. 126).

The early development and formation of the larval mouth and anus (p. 135) have already been dealt with. The enterocoel or coelom has the form of an anterior unpaired diverticulum of the enteron extending into the preoral lobe and sending back two lateral prolongations, one on each side of the larval gut (Fig. 98). This soon separates from the gut, and the posterior prolongations of it eventually meet one another ventrally, their opposed walls forming a ventral mesentery. The **primary water-pore** is now formed as a pocket of the unpaired portion of the coelom. It meets the skin of the dorsal surface just to the left of the middle line, and a perforation is formed at the point of contact. At the same time there is formed, first on the left side of the enteron and then on the right, a septum, by which the hinder parts of the two coelomic prolongations referred to above become separated off from the anterior part and form closed sacs called the right and left **posterior coeloms** respectively. The unpaired portion of the coelom, together with the anterior portions of the two prolongations, constitute the **anterior coelom** of the larva into which opens the primary water-pore.

The **hydrocoel** is developed as an outgrowth from the hinder end of the anterior coelom on the left side, and while it is yet but faintly marked indications of its five primary lobes appear. These, which are numbered* 1, 2, 3, 4, and 5, No. 1 being the most dorsal, are arranged in a curve open anteriorly, the hydrocoel sac assuming a horseshoe shape (Figs. 101, 102). The two limbs of the horseshoe eventually come together, enclosing the stalk of the preoral lobe and the oesophagus of the adult, when that is formed on the left side of the larva. In this way the circumoral water-vascular vessel is developed from the horseshoe-shaped hydrocoel. The radial canals are developed from the lobes of the hydrocoel. Shortly after the formation of the left hydrocoel or hydrocoel proper, a rudimentary *right hydrocoel* is developed as an outgrowth from the hinder wall of the anterior coelom to the right of the middle line (Fig. 101, *rhy*). It loses its connexion with the anterior coelom and persists into the adult as a small thin-walled sac beneath the madreporite.

* The relations of these numbers to the enumeration adopted for the adult is explained on p. 120. The numbering here adopted has relation to the fact that the hydrocoel before it closes to form a ring has two ends, one of which may be called anterior.

The **stone-canal** arises as a groove along the anterior face of the posterior wall of the anterior coelom. The central portion of this groove becomes closed to form a canal which opens at its posterior end into the hydrocoel between lobes 1 and 2 and at the other into the anterior coelom; which as we have seen opens to the exterior by the primary water-pore. Save for this communication the anterior coelom and the hydrocoel become completely separate. The anterior coelom persists into the adult as the **axial sinus**. When the primary water-pore becomes converted by subdivision into the numerous pores of the madreporite of the adult, most of these are found to lead directly into the stone-canal, but some open into the axial sinus. The stone-canal retains its opening into the axial sinus (anterior coelom).

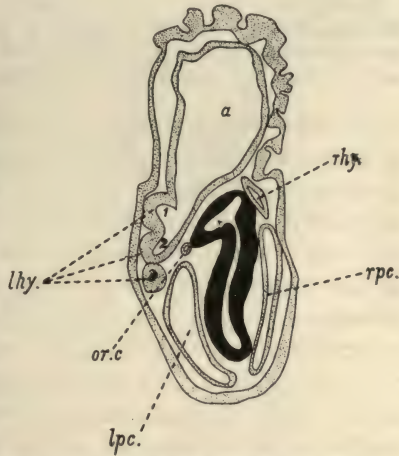


FIG. 101.—Longitudinal horizontal section of a larva of *Asterina gibbosa* showing the origin of the hydrocoel and the relation of the coelomic sacs (after MacBride). *a* anterior body-cavity in the preoral lobe; *lpc* left posterior coelom; *lhy* 1, 2, 3 lobes of the hydrocoel, no. 1 being the most dorsal, no. 3 the posterior, no. 5 (not shown) is at the other end of the incipient ring and is the most ventral; *or.c* oral coelom; *rhy* right hydrocoel; *rpc* right posterior coelom.

The left posterior coelom undergoes a very complicated development. It gives off dorsal and ventral outgrowths which grow on to the right side of the larval body, and a diverticulum which extends round the oesophagus and is called the *oral coelom*. These all become indistinguishable in the adult and merely persist as part of the perivisceral cavity. In addition to these the left posterior coelom gives off four interradiial prolongations, each of which bifurcates to proceed to the adjacent arm rudiments. These are the first traces of the outer **perihæmal ring** and of the **radial perihæmal canals** (Fig. 131). There is a fifth interradiial coelomic prolongation, viz. that which lies between lobe 1 and 2 of the hydrocoel and is distributed to arms 1 and 2; this lies in the interradius of the axial sinus and stone-canal and is an evagination of the anterior coelom. Lastly the **aboral sinus** is an outgrowth of the left posterior coelom, from which it becomes completely cut off in the adult (p. 146). The right posterior coelom remains much smaller than the left. It persists in the adult as the part of the body-cavity (sometimes called epigastric) which lies between the gut and the aboral body wall of the starfish. It is prolonged into each arm as the space between the two mesenteries of each pyloric caecum,

so that these mesenteries are really remains of the septum between the right and left posterior coeloms. In the central region of the disc this septum seems to have disappeared in the adult.

The anterior coelom, with the atrophy of the preoral lobe, becomes much reduced in size. As stated above, it persists as the axial sinus. The **inner perihæmal ring** is an outgrowth of the axial sinus, with the ventral end of which it remains continuous (Fig. 105, *int.p.r.*).

The **axial organ** makes its appearance as a ridge projecting into the axial sinus and containing jelly, fibres and leucocytes. Later there is formed a thickening of the epithelium of the left posterior coelom near the aboral end of the incipient axial organ. The cells of this thickening are the primitive **germ-cells**. They become invaginated into the septum separating the axial sinus from the left posterior coelom, and thence grow out in two directions, viz. (1) into the ridge of the axial organ forming its core, and (2) as a cord extending in a direction parallel to the surface of the disc and constituting the **generative rachis**. The generative rachis becomes enclosed by a flap of peritoneum in a space cut off from the left posterior coelom and known as the **aboral sinus**. It forms an aboral ring on the dorsal side of the stomach and sends off, as it passes each interradius, two branches enclosed in corresponding branches of the aboral sinus. These branches end in swellings which become hollowed out, acquire a communication with the exterior and form the **generative glands**. The portion of the aboral sinus round the gonads becomes cut off by a septum from the rest.

The **metamorphosis** of *Asterina gibbosa* begins on the eighth day of its development. The larva fixes itself by its preoral lobe to the substratum by means of a thin mucilage which appears to be secreted by the adhesive disc, and it remains attached during the whole of the metamorphosis (Figs. 102 to 104). The following changes occur :—(1) The constriction of the body into disc and stalk, the latter being formed from the preoral lobe. (2) The sharp flexure of the disc on the stalk, the disc being bent obliquely and to the left, so that the left side of the body is turned towards the substratum. (3) The preponderating growth of the organs of the left side, the left posterior coelom and the left hydrocoel having both sent out dorsal and ventral horns, which meet so as to form complete circles, while the right hydrocoel and the right posterior coelom remain small. (4) The gradual atrophy of the stalk. (5) The out-

growth of the adult oesophagus and the formation of the new mouth on the left side.

Even before the metamorphosis the lobes of the hydrocoel are visible on the left-hand side of the larva in a curve open anteriorly (Fig. 102), the dorsal lobe being no. 1, the posterior no. 3 and the ventral no. 5. On the right side are visible the first rudiments of the arms, lettered *A-E*, the dorsal being *A* and the ventral *E*; these arm rudiments are developed over the left posterior coelom. The open curve of the hydrocoel eventually closes into a circle, the two ends coming together round the base of

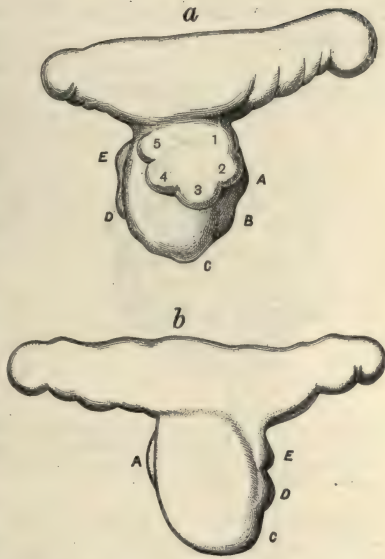


FIG. 102.—Larva of *Asterina gibbosa* at the commencement of the metamorphosis (about eight days), *a* from the left side; *b* from the right (after Ludwig, from MacBride). The larval organ has disappeared. The arabic numerals denote the primary lobes of the hydrocoel, the letters *A-E* the rudiments of the arms.

the preoral lobe (stalk), so that the preoral lobe arises from the oral surface of the developing disc (Fig. 105). In this closure the rudiment of arm *E* shifts so that it comes to lie directly on lobe no. 1 of the hydrocoel. When this fitting together of the two surfaces of the future disc is complete, the oral and aboral surfaces of the starfish are fashioned, and it is seen that the oral surface is derived from the left and slightly ventral side of the larva, the aboral from the right and slightly dorsal side. Meanwhile the first calcareous plates are laid down on the aboral surface as shown in Fig. 104 *B*, on the oral surface in Fig. 104 *A*. The *terminals*, as will

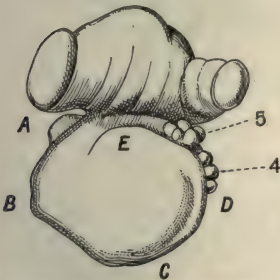


FIG. 103.—Larva of *Asterina gibbosa* of nine days from the right side. The letters denote the rudiments of the arms, the arabic numerals the lobes of the hydrocoel. The first formed tube-feet have been budded out from the hydrocoel lobes (from MacBride, after Ludwig).

Meanwhile the first calcareous plates are laid down on the aboral surface as shown in Fig. 104 *B*, on the oral surface in Fig. 104 *A*. The *terminals*, as will

be seen, are developed on the aboral side, but over the left hydrocoel.

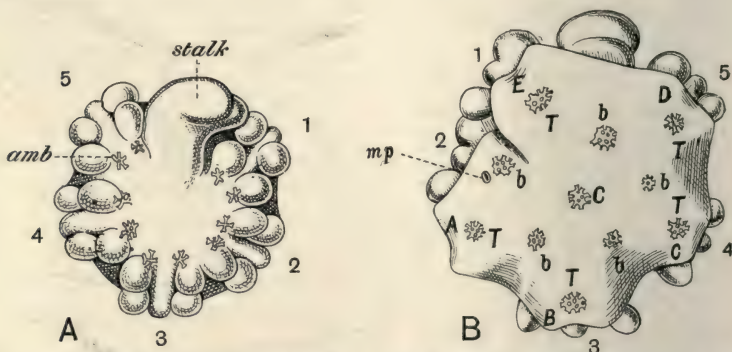


FIG. 104.—The just metamorphosed starfish of *Asterina gibbosa*, about ten days old; *A* oral view; *B* aboral view (from MacBride, after Ludwig). *amb* ambulacral ossicles; 1-5 the lobes of the hydrocoel; *A-E* the arms; *b* the basal plates; *c* the central; *mp* the madreporic pore; *T* the terminals.

The development of Asteroids with a bipinnaria larva is very similar to that of *Asterina*. The principal difference seems to consist in the fact that in bipinnaria (Goto, Bury, Field, *op. cit.*) the coelom early becomes

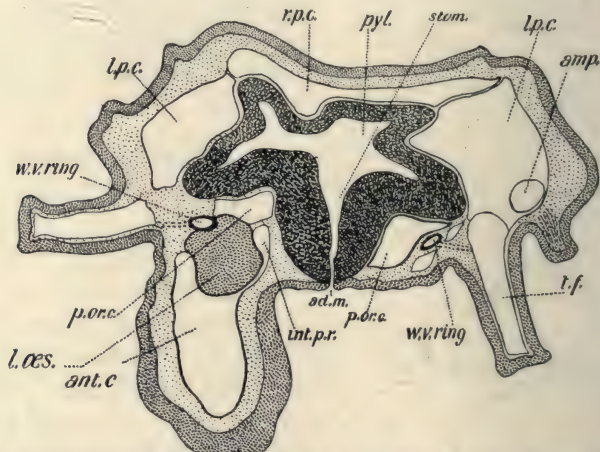


FIG. 105.—Longitudinal vertical section through a metamorphosing larva of *Asterina gibbosa* (after an original drawing by E. W. MacBride). The section passes through the interradius of the preoral lobe and through the opposite radius, and shows that the preoral lobe of the larva is attached to the oral surface of the adult. *ad.m.* adult mouth; *amp.* ampulla of a tube-foot; *ant.c.* anterior coelom in the preoral lobe; *int.p.r.* internal pericardial coelom; *l.oes.* vestige of larval oesophagus; *l.p.c.* left posterior coelom; *p.o.c.* pericardial coelom; *pyl.* pyloric sac; *r.p.c.* right posterior coelom; *stom.* stomach; *t.f.* tube-foot; *w.v.ring* water-vascular ring canal.

completely double (Fig. 106), whereas in *Asterina* the anterior coelom is single from the first, the posterior alone being double. Later, after the division of the coelom into anterior and posterior in bipinnaria, the two

anterior coeloms unite in the front part of the preoral lobe to form a single cavity.*

In bipinnariae with brachiolar arms, which as it will be remembered processes of the preoral lobe, temporary fixation† during development takes place by these arms. During the metamorphosis of bipinnariae fixation occurs by means of a median oval sucker-like disc on the preoral lobe (p. 141). Attachment by the preoral lobe has also been noticed by Perrier in *Asterias spirabilis*, in which the larvae adhere to the buccal membrane of the mother.

From the above account‡ it is clear that in the larvae of Asteroids which become attached during development, the fixation is effected by the preoral lobe, and that the stalk so formed is surrounded by the hydrocoel and springs from what will become the oral surface of the starfish. The knowledge of this fact, so important for a proper comprehension of the morphology of the class, we owe to MacBride. The further statement may be made that the coelom, which arises by a single diverticulum from the enteron, becomes segmented into three pairs of chambers, viz. the anterior coelom, the hydrocoel, and the posterior coelom. Of these the anterior coelom is at first single or soon becomes so, and, as in the Enteropneusta, acquires an opening or two openings to the exterior (water pores). Of the second pair the chamber of the left side becomes much larger than that of the right, retains its connexion with the anterior chamber by the stone-canal, and becomes the hydrocoel, while the right remains as a small apparently functionless sac; this pair of chambers may be compared to the collar-cavities of the

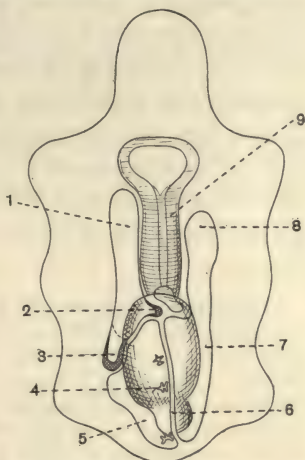


FIG. 106.—Optical section of an Asteroid larva (Bipinnaria) seen from the dorsal surface (after Bury). There are two anterior coelomic sacs, the water pore is shown opening into the left of them. The hydrocoel is indicated but not yet completely separated from the left anterior coelom. 1 left anterior coelom; 2 water pore; 3 hydrocoel; 4 second terminal plate (arm B); 5 left posterior coelom; 6 mesentery separating the two posterior coeloms; 7 right posterior coelom; 8 right anterior coelom; 9 enteron.

* There are according to Field (*op. cit.*) two water-pores in many of the bipinnariae of *Asterias vulgaris*, but it is doubtful if this can be regarded as a normal occurrence (see note, p. 166).

† Bury, *op. cit.*, 1895; Delage, *Arch. Zool. Exp.* (4), (2), 1905, p. 27.

‡ The preceding account of the development of *Asterina* is taken largely (often directly quoted) from the important work of MacBride (*loc. cit.*).

Enteropneusta, which in the Cephalodiscida furnish the tentacles. The chambers of the third pair both persist and furnish the perivisceral cavities of the adult, but the left becomes, in accordance with the predominance of the organs of the left side of the larva, much larger than the right, and alone furnishes the germ cells from its lining. The knowledge of these facts we owe mainly to Bury and MacBride. Bury was the first to grasp the importance of the anterior coelom and its transference into the axial sinus, while MacBride went a step further in showing that the coelom was segmented into three chambers on each side, though Metschnikoff * preceded him in having demonstrated the presence of the right hydrocoel in *Amphiura squamata*.

In Echinoids (Fig. 99) the single enterocoel divides into two, one on each side. Each of these again divides into two, the hindmost of which lie at the sides of the stomach and constitute the posterior coeloms. The left anterior division develops a water-pore, which is placed on the left side of the dorsal surface, and then becomes constricted into two parts, of which the anterior retains the water-pore and persists into the adult as the madreporitic ampulla and axial sinus, corresponding to the left anterior coelom of Asterids, while the posterior becomes the left hydrocoel. The separation between these two vesicles appears not to become complete, the connecting tube persisting as the stone-canal. The left hydrocoel has at first the form of a disc which is soon transformed into a ring (apparently by becoming notched on one side) through which the adult oesophagus later grows. The right anterior division likewise constricts into two parts, but does not develop a water-pore. The anterior of these is the right anterior coelom; its fate is unknown. The posterior portion is the right hydrocoel, which remains small, never develops lobes, and persists into the adult as the "dorsal sac" which lies beneath the madreporite. The segmentation of the coelom therefore proceeds in a very similar manner to that of Asterids, and as in them the segmentation of the left side precedes that of the right. The two posterior coeloms give rise to the general perivisceral cavity.

The lantern coelom, which is homologous with the outer periaemal ring of Asterids, develops as five evaginations of the left posterior coelom. The teeth and jaws are developed from the walls of these pockets and the radial periaemal canals are outgrowths of them. The genital rachis, genital organs and aboral sinus are developments of the left posterior coelom, exactly as in Asterids. An invagination of ectoderm which becomes closed is formed on the left-hand side of the larva. Its cavity is known as the **amniotic cavity**, its outer wall becomes thin and is called the amnion, while its inner wall or floor applies itself to the hydrocoel and forms the ambulacral surface of the adult. The epineural canals are developed as invaginations of the floor of this cavity. There is no fixation of the larva during the metamorphosis. Lastly it must be men-

* Studien üb. d. Ent. d. Echinodermen u. Nemertinen, *Mém. de l'Acad. de St. Petersbourg*, 14, 1869.

tioned that there is a well-developed nervous system in the larva of *Echinus*. It has the form of an apical plate of neuro-epithelium, placed on the preoral portion of the body dorsal to the ciliated band and between the preoral arms. It is not recognizable till the larva is three weeks old.

In the metamorphosis the animal falls to the bottom, the amnion ruptures and shrivels up, the larval arms are absorbed by phagocytic amoebocytes, the larval mouth and anus close and the somewhat spherical form of the adult is assumed. At first the metamorphosed animal is without a mouth and anus; these soon appear, the mouth first. The anus is formed in the centre of the antambulacral surface which is at first equal in area to the ambulacral.

In Ophiurids a single coelomic sac is budded off from the anterior end of the archenteron. This soon divides into a right and left sac. Each of these divides into anterior and posterior coeloms. The hydrocoels

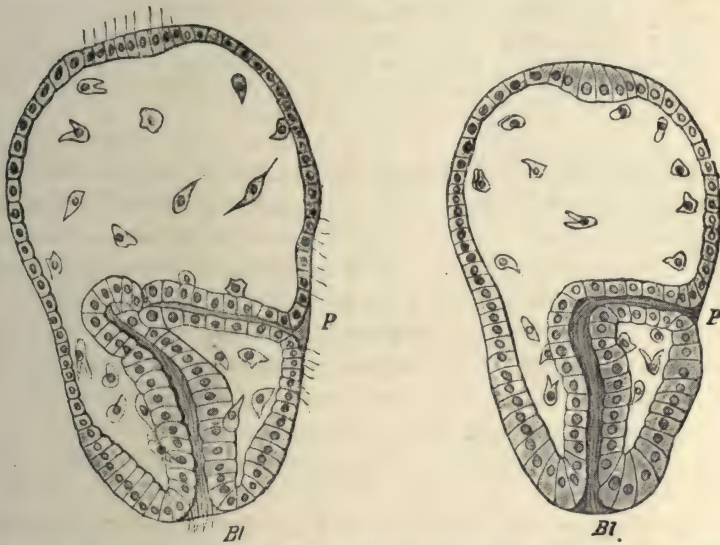


FIG. 107.—Longitudinal vertical sections of the two stages of the larva of *Synapta digitata* showing the formation of the enterocoel and of the primary water-pore *P*. *Bl* blastopore (after Selenka).

then arise from the hind end of the anterior coelom in the usual way (MacBride) and the left anterior coelom develops a water-pore. The left hydrocoel alone acquires lobes and develops into the water-vascular system. As in *Asterina* the rudimentary right hydrocoel in abnormal specimens occasionally acquires a form similar to the left.

In Holothurians the single pouch acquires an opening to the exterior by a pore placed on the dorsal surface and just to the left of the middle line. This is the **primary water-pore**. In *Synapta* it may even be formed before the enterocoel has separated from the enteron (Fig. 107). Soon after the formation of the pore, the enterocoel divides into two portions, an anterior and a posterior; the anterior remains in connexion with the water-pore and constitutes the combined anterior coelom and hydrocoel, while the

posterior is the splanchnocoel. The splanchnocoel then divides into two sacs which apply themselves to the gut, one on the right and the other on the left, and give rise to the perivisceral cavity and its lining. The tube connecting the combined anterior coelom and hydrocoel with the water-

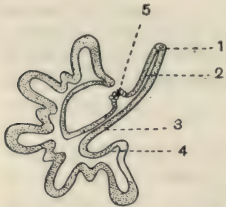


FIG. 108.—Diagram of the hydrocoel and anterior coelom of an old Holothurian auricularia (after Bury). 1 water-pore; 2 pore canal; 3 sand-canal; 4 polian vesicle; 5 anterior coelom.

pore elongates and a small swelling appears on its anterior wall (Fig. 108). This is supposed to be the reduced anterior coelom. The vesicle itself becomes lobed and forms the hydrocoel. It eventually surrounds the oesophagus to form the circumoral water-vascular vessel and gives off five outgrowths which become the radial canals. The canal connecting the hydrocoel with the small anterior coelom must be regarded as the stone-canal. In the forms with a so-called internal madreporite, it must be supposed that the canal (water-pore) distal of the small anterior coelom breaks down and that the anterior coelom acquires a free communication with the general perivisceral cavity by the rupture of its walls, as it does in Crinoids (p. 158).

Development of Crinoids. The development of Crinoids differs considerably from that of the other classes and requires separate treatment. The principal points of difference concern (1) the form of the larva; (2) the relation of the larval preoral lobe to the adult surfaces; (3) the fact that, though the hydrocoel at first undergoes a displacement to the left side, the oral surface of the adult is the posterior surface of the larva and the left posterior coelom does not exceed the right in size; (4) the posterior coeloms arise from the enteron independently of the common rudiment of the anterior coelom and hydrocoel; and (5) the absence of any trace of a right hydrocoel.

In *Antedon*, the only Crinoid the development of which is known, the egg, as in most other Echinoderms, is fertilized and undergoes its whole development in the sea-water, but it remains for some time within the vitelline membrane attached to the pinnules of the parent. The total cleavage leads to the formation of a hollow blastosphere from which a gastrula arises by invagination. The blastopore closes completely at or near the hind end of the embryo, and the uniform ciliation gives place to five ciliated bands which encircle the body transversely and to a ciliated tuft at the anterior end (Fig. 109). The ciliated tuft springs from a thickened patch of ectoderm which constitutes a *neural apical plate*. In the deeper layers of this neural plate nerve-cells and fibres are formed and constitute the larval

nervous system. The embryo usually leaves the egg-membrane on the seventh day, and becomes the free-swimming larva, which shows bilateral symmetry, the ventral surface being slightly flattened.

The anterior ciliated ring is incomplete ventrally, and between the second and third, which are separated by a wider interval than the others, there is a ciliated depression (*Lm*), called the vestibular depression (so-called larval mouth) and supposed to correspond with the now closed blastopore. On the ventral surface between the first and second rings, there is a small pit, the adhesive pit (*Gr*), by the secretion of which the larva, after a free-swimming life of from 12 to 48 hours, attaches itself. After attachment the larva at first lies with its entire ventral surface turned towards the surface to which it is attached; soon however it erects itself and projects at right angles to the substratum. The attached, i.e. anterior, end of the larva now becomes narrow and elongated into the stalk, while its free, i.e. posterior, end becomes broader and constitutes the rudiment of the calyx (Fig. 115). The vestibular depression has during these changes become cut off from the ectoderm and forms a closed ectodermal vesicle (Fig. 114, 4), which constitutes the larval vestibule. At first this vesicle is placed on the ventral surface, but soon it comes to occupy the free end (Fig. 115). This change in position is shared by certain internal organs, and is doubtless due to the relative growth of parts by which the ventral surface of the larva comes to occupy the free end. The floor of the vestibule applies itself to the adjacent internal organs and eventually becomes perforated by the mouth opening. Meanwhile processes from the water-vascular ring, the tentacular canals, push before them the floor and project as tentacles into the cavity of the vestibule. Eventually the roof of the vesti-

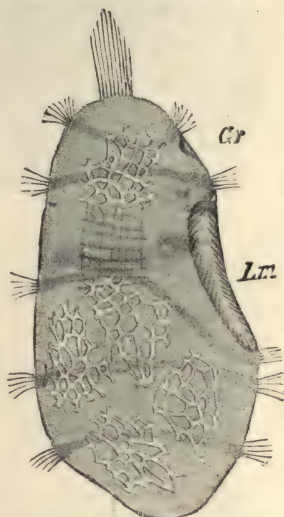


FIG. 109.—Larva of *Antedon rosacea* with ciliated bands, anterior tuft of cilia and rudiments of the skeletal plates (from Korschelt and Heider). *Gr*. adhesive pit by which the larva attaches itself; *Lm*. the vestibular depression (larval mouth).

bule disappears and the tentacles and mouth become freely exposed. We thus reach the so-called Cystid stage of development (Fig. 110).



FIG. 110.—Cystid larva of *Antedon* (after Thomson).

The larvae of Crinoids, then, become attached by the ventral side of the anterior end, and, as was shown by Bury, the stalk of the adult is a development of the preoral lobe. They therefore resemble the larvae of Asterooids in the fact that attachment takes place by the preoral lobe, but differ entirely from them in the relation which the preoral lobes bear to the arrangement of the organs in the adult; for whereas in Asterooids the preoral lobe is encircled by the water-vascular ring, and its withered vestige springs from the oral surface of the adult disc (Fig. 105), in Crinoids it is quite free of the circum-

oral vessel and arises from the apical or aboral surface of the adult.

Our knowledge of the development of the coelom is mainly due to Bury, who in his memoir on the development of

*Antedon** first made us familiar with the conception of the anterior coelom and so paved the way for the modern views, largely due to him and MacBride, on the segmentation of the coelom into three chambers on each side of the body (p. 149).

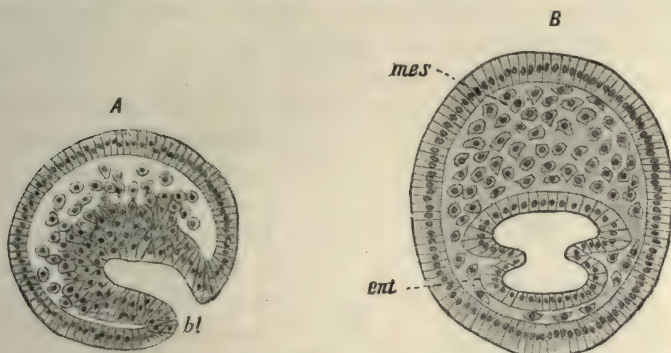


FIG. 111.—*A* longitudinal vertical section of gastrula of *Antedon* at the end of the second day showing the formation of mesenchyme. *bl* blastopore (after Bury). *B* longitudinal section of a later stage showing the division of the archenteron. *mes* mesenchyme; *ent* first-formed enterocoel which gives rise to the right and left posterior coeloms (after Barrois).

After the closure of the blastopore the archenteron which is placed at the hind end of the embryo divides by a constriction into an anterior and a posterior portion (Fig. 111 *B*). The posterior portion is the first enterocoel vesicle; it lies close to the hind end of the embryo and soon divides into a right and left part, which constitute the right and left posterior coeloms respectively. The anterior portion or vesicle into which the archenteron has divided develops two outgrowths, a dorsal and a ventral (Fig. 112, 5, 7), which give origin to the intestine; and itself becomes constricted into two portions, a ventral one which is the rudiment of the hydrocoel, and an anterior one which is the anterior coelom (Fig. 112). These become separated, in

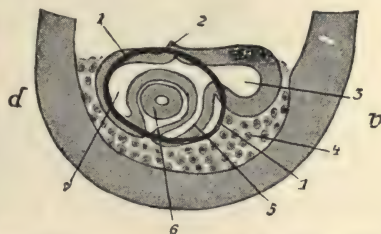


FIG. 112.—Posterior end of an embryo of *Antedon* of sixty hours, from the right side. 1 the outline of the right posterior coelom; 2 rudiment of anterior coelom; 3 rudiment of hydrocoel; 4 mesenchyme; 5 ventral, 7 dorsal part of enteron, which clasps 6 the still persistent connecting portion between the incipient right and left posterior coeloms (from Lang, after Seeliger).

* *Phil. Trans.*, 179, 1888.

continuity with one another, from the rudiment of the intestine. Soon after this has happened the anterior coelom separates from the hydrocoel, which, placed between the enteron and the ectoderm on the left-hand side of the body (Fig. 113), at once acquires the characteristic horseshoe form. The anterior coelom then acquires its external opening, the water-pore, which is placed on the left side of the body just in front of the fourth ring of cilia. Later the hydrocoel develops an anteriorly

directed outgrowth which acquires an opening into the anterior coelom and forms the **stone-canal**.

The posterior coeloms now shift; the left-hand one moves posteriorly and comes to lie like a cup over the hind end of the enteron (Fig. 113, 5), while the right sac extends anteriorly and following the enteric wall reaches on to the left side (Fig. 114). The right posterior coelom gives off from its anterior end five forwardly directed diverticula (Fig. 113, 2).

These become cut off from it at a later stage, and give rise to the **chambered organ**.

The calcareous plates make their appearance in the embryo on the sixth day. They are shown in Fig. 114, which however is taken from a larva after attachment.

There are five *orals* (Fig. 114, *or*) arranged in a horseshoe curve near the posterior end. The horseshoe is set obliquely to the long axis, its dorsal end being posterior to its anterior end, and the open end of it is directed ventrally. Parallel to this row, but anterior, are the five *basals* (*ba*) set in a similarly disposed horseshoe curve. Both the orals and basals are, as shown by the later development, interradially placed. In front of the basals

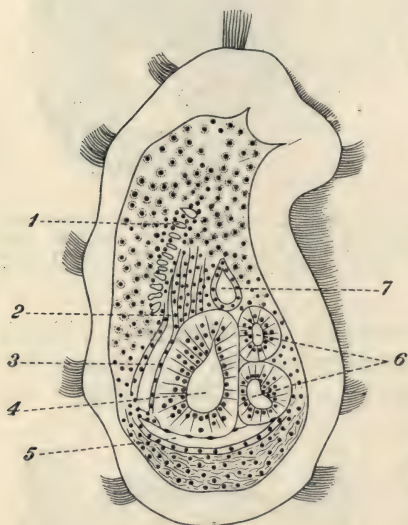


FIG. 113.—Longitudinal-vertical section of a free-swimming larva of *Antedon*. 1 stem-joints; 2 anterior prolongation of right posterior coelom to form the chambered organ; 3 right posterior coelom; 4 enteron; 5 left posterior coelom; 6 hydrocoel; 7 anterior coelom.

but deeper and in the axis of the body is a row of stem-joints. The anterior of these is the **dorsocentral** (Fig. 114, 1), which becomes the terminal joint of the stem. The stem-joints rapidly increase in number, the new pieces being added at the posterior (proximal or calycine) end of the row. A little later, on the seventh day, the underbasals (*ib*), three in number (rarely four or five), are formed. They lie in front of the basals and a good deal deeper and eventually fuse with the top (posterior) stem joint to form the **centro-dorsal plate**.

At about this stage the larva hatches and undergoes its brief free-swimming life. It then attaches itself (p. 153), the ciliary rings, preoral tuft and apical plate atrophy, and the anterior end begins to become narrower and longer, and to mark itself out as the stem from the posterior end, which becomes the calyx. In fact the larva becomes club-shaped, the swollen free end forming the rudiment of the calyx (Fig. 114).

The vestibular depression (p. 153) on the ventral surface becomes deeper and converted into an ectodermal invagination

which occupies the greater part of the ventral surface, remaining open for some time anteriorly. It eventually closes, and soon after attachment shifts on to the posterior end of the larva (Fig. 115, 5). The hydrocoel follows this shift of the vestibule and lies at the posterior end immediately beneath the floor of the vestibule (Fig. 114, 3). It is still an open horseshoe, the opening being towards the water-pore; but its ends have approximated and its five lobes, each of which soon becomes trilobate, pushing up the ectoderm of the floor of the vestibule, project into the vestibular cavity as the primary tentacles. Five additional pairs of tentacles are formed later at the base of these (Fig. 115, 7).

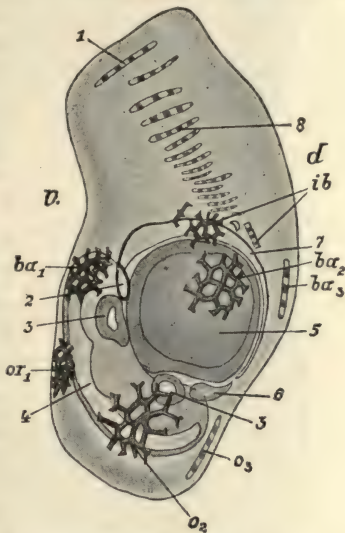


FIG. 114.—Young attached larva of *Antedon* from the left side (from Lang, after Seeliger). The vestibule is closed. *ba* 1–3 basals; *or* 1–3 orals; *ib* underbasals; 1 dorsocentral plate; 2 anterior coelom; 3 lobes of hydrocoel; 4 vestibule; 5 enteron; 6 left, 7 right posterior coelom; 8 stem-joints; *v* ventral; *d* dorsal surface of the larva.

The mouth is formed as a funnel-shaped depression of the vestibule, which passes through the hydrocoel ring and opens into the enteron (Fig. 115, 8). On the shifting of the vestibule

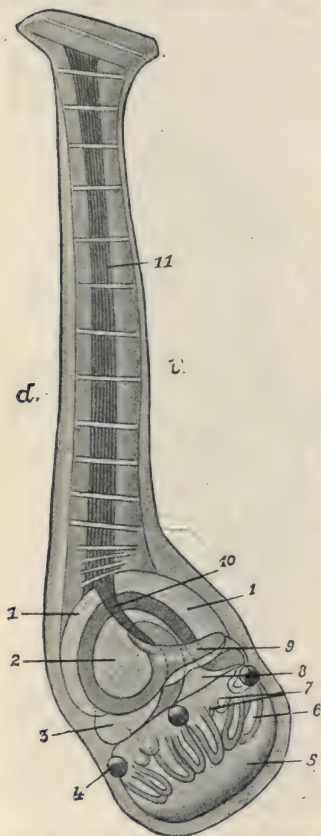


FIG. 115.—Attached larva of *Antedon* after the separation of the stalk and calyx (from Lang, after Seeliger). The calcareous plates are not shown. *d* dorsal, *v* ventral side. 1 right posterior (aboral) coelom; 2 stomach; 3 left posterior (oral) coelom; 4 sacculi; 5 vestibule; 6 primary tentacles, 15 in number derived from the 5 lobes of the hydrocoel each of which becomes 3-lobed; 7 the secondary interradial tentacles (in 5 pairs); 8 oesophagus; 9 hind gut; 10 axial organ; 11 fibrous strands in the stalk.

to the hind end, the oral plates which, like the basals, have become arranged in a circle, also shift backwards. They come to lie in the thin roof of the vestibule, and when the latter ruptures and splits into five lobes, each lobe contains one oral plate. The stage we have now reached is sometimes called the **cystid stage** (Fig. 116, *b*). It is characterized by having a mouth overhung by five oral plates, an absence of arms, and an anus which has been formed as a lateral perforation through the body wall outside the circle of the orals. There are twenty-five tentacles, which at first arose in five groups, but now all spring separately from the water-vascular ring.

As to internal changes, we may mention that the mesenteries between the right and left posterior coeloms, which, by shifting, have some time before become aboral and oral, break down so that the perivisceral cavity is a continuous cavity. Further, the anterior coelom loses its walls and becomes merged in the general body-cavity. The result of this is that the primary water-pore and the sand-canal, which at the previous stage

both opened into the anterior coelom, now open directly into the body-cavity. The primary water-pore and the anus lies in the same interradius. Later each of the other interradii

acquires a water-pore and sand-canal which lead from their first appearance into the general body cavity.

The **genital stolon** (axial organ) develops as a thickening in

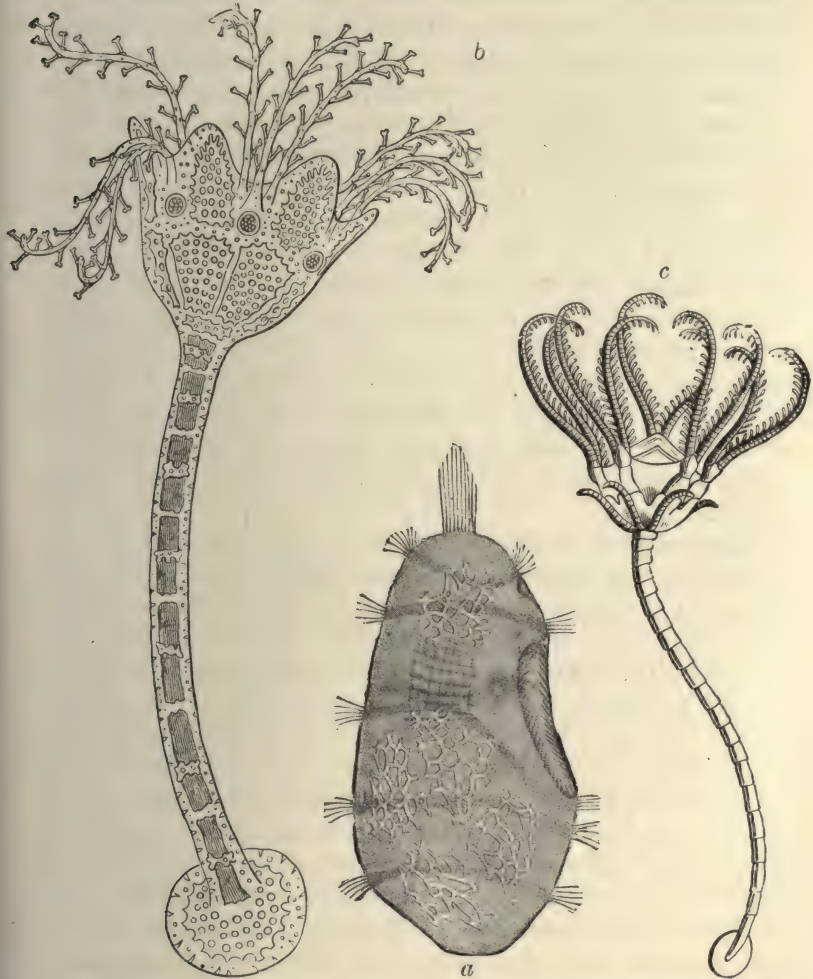


FIG. 116.—Larvae of *Antedon* (after Thomson). *a* free-swimming larva with rings of cilia; *b* attached cystid stage; *c* older stage described as *Pentacrinus europaeus* with arms and cirri.

the epithelial wall of the aboral coelom. The genital rachis is probably developed as an outgrowth of this.

The larva becomes converted into the pentacrinoid larva

(Fig. 116, c) by the formation of the arms, which grow out from the sides of the body aborally to the water-pore and anus and between the oral and basal plates. The result of their outgrowth is that the oral surface of the body is much enlarged by the formation of the tegmen calycis beyond the circle of the oral plates which become reduced in size and eventually disappear. On the aboral side of the calyx, calcareous plates, the radials, are formed to support the growing arms. Finally the calyx becomes detached from the stalk, and the free adult state is reached.

The Crinoids, in so far as relates to the development of the coelom, differ from all other Echinoderms in the fact that the rudiment of the posterior coeloms is budded off from the gut independently of the anterior coelom and hydrocoel. They resemble certain of the Holothurians in the fact that the anterior coelom becomes merged in the general body cavity, but differ from these in the retention of the water-pore. In becoming attached by the preoral lobe they resemble the larvae of certain Asterids, but they differ, as already explained (p. 154), from these in the relation which the attaching surface bears to the adult structure.

Affinities. The fundamental fact in the morphology of the Echinoderms is the enterocoelic origin of the coelom. In this, as has been already pointed out in the second volume of this work (chap. i., p. 7) they are associated with the Brachiopoda Chaetognatha, Chordata and probably the Phoronidea. Whether we are to regard this fact as indicating affinity it is difficult to say. In the absence of evidence tending to unite any of these groups more closely or as closely with any other group of the animal kingdom, we may perhaps consider this common feature as sufficient justification for treating them in immediate succession to one another, but we must not attribute too much importance to it, for it is absent from both vertebrate and tunicate development, nor is it found in Annelids, Arthropods and Molluses, the coelom of which is clearly the homologue of the coelom of enterocoelic forms. The question now presents itself, do the Echinodermata possess any features which enable us to associate them more closely with any particular phylum of the Enterocoela than with the others? It has been pointed out by some zoologists, amongst whom I may specially mention MacBride, that in the primitive disposition of their coelomic

sacs they present a certain resemblance to the Chordata. In all the members of that great group with the exception of the Tunicata, the coelom in its first state in the embryo presents traces more or less marked of three divisions : these are (1) the anterior or proboscis coelom, which in Vertebrata and Enteropneusta is single, in Amphioxus double, (2) the collar or middle coelom which is always double, and (3) the trunk coelom which is double and which in Vertebrata and Amphioxus becomes metamerically segmented. In Echinodermata we seem to be able to make out indications at least of a similar tripartite division. We have (1) the anterior coelom which is sometimes single (*Asterina*), sometimes double (*Echinus*), (2) the hydrocoel which is probably fundamentally double though in some cases only one hydrocoel sac is formed (Holothurians, Crinoids), and (3) the posterior coelom which is always paired. Of these the hydrocoel presents the peculiarity of growing out into tentacles—a feature which is also presented by the middle division of the coelom in the enteropneust genera, *Cephalodiscus* and *Rhabdopleura*. But with these similarities we have to note certain differences. In the first place in the Chordata, in which the enterocoelic origin of the coelom is clearly presented, these three divisions of it always come off from the enteron separately, whereas in Echinoderms the enteron at most gives off only one pair of coelomic sacs. Further, whereas in the Chordata the middle coelom (collar) is never associated more closely with the anterior than with the posterior, in the Echinoderms it is always closely associated with the anterior coelom, being developed from it and remaining connected with it by the stone-canal throughout life. With regard to these differences we have only to say this : that they are differences such as we might expect from the greater remoteness of the Echinoderms from the Chordata than of any of the Chordata from each other, but that they are not sufficiently great to put out of court the homologies suggested by the comparison.

To turn to other points of resemblance : we have the resemblance (1) in the central nervous system, (2) in the skeletal system, (3) in the shifting of the mouth and in the asymmetry of the body, and (4) in the larval form. To take these in order : (1) In the Chordata, as is well known, the central nervous system

never becomes separated by mesodermal tissues from the tract of ectoderm which gave it origin in the embryo. This is a feature of all Echinoderms in so far as the ventral nervous system, which is the predominant central nervous system, is concerned. When this nervous system is removed from the surface, the removal is effected by invagination (p. 124).

(2) The presence of calcified skeletal tissue in the mesoderm of the body wall is a character found in Echinodermata and Vertebrata alone among Coelomata. This has already been pointed out by MacBride, and though not perhaps a very important indication of affinity is one which from its rarity deserves mention here.

(3) In all Echinoderms the mouth shifts from the ventral surface of the larva on to the left side of the body. This can be demonstrated in all classes except Crinoids, and in Crinoids it may fairly be inferred. In Chordates a similar though not identical phenomenon is presented by *Amphioxus*. In this animal the mouth actually makes its appearance on the left side in an animal otherwise bilaterally symmetrical, but the phenomenon differs from that of Echinoderms in the fact that the left-sided position of the mouth is not preceded by a condition in which it is in the middle ventral line. The feature then which Echinoderms have in common with *Amphioxus* is the sinistral position of the mouth. Here again we have a character which strikes us from its very rarity, for it is found in no other Coelomate nor so far as we know in any other member of the animal kingdom. It also strikes us by its strangeness and inexplicableness. In *Amphioxus* no serious attempt has been made to explain it.

In attempting to explain peculiarities of this kind we are accustomed to take into consideration two factors which must be kept distinct. Firstly we have peculiarities in habit, secondly associated peculiarities in other organs. Now in *Amphioxus* the asymmetry of the mouth is accompanied by no peculiarity in habit, for the animal while it has this monstrous mouth behaves more after the fashion of a bilaterally symmetrical animal than it does in later life, when the mouth has acquired a more median position and it has taken to burrowing in sand. Nor do the peculiarities in some of the other organs lend us any assistance, for no one, so far as we know, has ever attempted to bring the

extraordinary features in the development of the gill clefts, of the endostyle, of the head-cavities, the asymmetric position of the anus and olfactory pit, into relation with the asymmetry of the mouth. The thing cannot be done. There is no sort of connexion between these various asymmetries. They seem to occur without rhyme or reason. The mouth which should be a median structure is from the first on the left side; the gill-clefts, which are on the left in the adult, appear in the median line and at once pass on to the right side; the endostyle which is a median structure in the adult appears as an entirely dextral organ.

In Echinoderms on the other hand the asymmetry of the mouth is accompanied by changes in habit and by change of other organs which seem to be connected with the change in the mouth. The animal here becomes sessile or semi-sessile and acquires an entirely different symmetry in which other organs of the body participate in an intelligible manner. But though we can understand to a certain extent that the shift of the mouth might indent the left hydrocoel and bring about an inequality in the posterior coeloms, no adequate attempt has ever been made to show how the sessile habit and the radial structure is connected with the shifting of the mouth on to the left side. We have here three factors: the sinistral mouth, the radial structure and the sessile habit. Can these factors be brought into the relation of cause and effect?

(1) Can the sessile habit be regarded as the cause of the other two, even if we accept the view that all Echinoderm classes have passed through a fixed stage in their phylogeny. We can only point out in reply that no such results have followed fixation in any other group of the Coelomata: they have not followed in Cirripedes, Brachiopods or in Tunicates.

(2) Can the left-handed mouth be regarded as the cause? In *Amphioxus*, the only other animal in which the mouth is sinistral, it is accompanied neither by the sessile habit nor by the radial symmetry.

(3) Lastly, can the acquisition of radial symmetry, to whatever cause due, have brought in its train the shifting of the mouth and the sessile habit? In the only other animals which can lay claim to a radial symmetry, the Coelenterata, no such result has followed.

It is therefore no more possible to explain the sinistral position of the mouth in Echinoderms than it is to account for the same phenomenon in Amphioxus. But that conclusion does not in any degree diminish the importance of the character as an indication of affinity. On the contrary it increases it. For, if it cannot be shown to be connected with habit of life or with other peculiarities of structure in the animals presenting it, the presumption that it is a property which was possessed by the ancestral matrix from which Echinoderms and Amphioxus have emerged is increased. We are thus brought back to the question which we touched upon on p. 116, are the Echinoderms descended from asymmetrical or from bilaterally symmetrical forms? This discussion of the asymmetry of Amphioxus and Echinoderms has elicited facts which are not without a bearing upon this question. We have seen that in Amphioxus there is hardly a single organ of the body which displays complete bilateral symmetry at all stages of existence, and in the adult traces of this asymmetry—slight traces, it is true, but all the more striking on that account—are present (position of olfactory pit and anus just to the left of the middle line, preoral hood and other small distortions). We have also seen that the asymmetry of one organ is entirely independent of the asymmetry of the others. Very similar statements may be made about Echinoderms: in these also development begins with a transitory bilateral symmetry which is almost at once followed by asymmetry, at least of the internal organs, and the asymmetry then initiated is never completely got rid of, for the radial symmetry of the adult is in all classes imperfect (least so in Holothurians), and some of the adult distortions, such as the position of the anus, recall the similarly slight distortions found in the adult Amphioxus. Now the upshot of these considerations is to make us pause in accepting as final the conclusion that the ancestral Echinoderm was a bilaterally symmetrical animal.

(4) The striking resemblance of the bipinnaria larva to the tornaria of Enteropneusta has already been referred to (p. 99). It is impossible to estimate its value, but it clearly cannot be passed over in a discussion of this kind, and taken in conjunction with the other facts mentioned must be admitted to have considerable weight.

We have now passed in review all the points of resemblance

between the Echinodermata and the Chordata and we have seen that they all, except possibly the last, are concerned with fundamental, not superficial, traits. Some of them link the Echinoderms to all the Chordates or to all except the Tunicata, e.g. the relations of the central nervous system and the general relations of the coelomic sacs ; another they hold in common only with Vertebrata, viz. the presence of calcified plates in the mesoderm of the body wall ; a third—the sinistral position of the mouth—is found again only in *Amphioxus* ; and lastly there is the striking resemblance to *Enteropneusta* by the tornaria larva. The accumulated weight of these facts is overwhelming and leaves us no choice but to consider not only that the Chordata are the nearest allies of the Echinodermata, but that the Echinodermata are of all Coelomata the nearest to the Chordata.

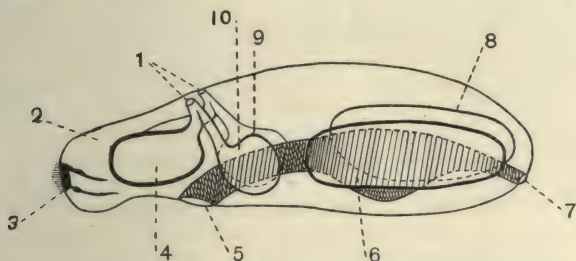


FIG. 116bis.—Diagrammatic representation of the supposed *Dipleurula* ancestor of Echinoderms, seen from the left side, with the ventral surface towards the substratum (after Bather). 1 right and left water-pore ; 2 preoral lobe ; 3 nerve plate of preoral lobe ; 4 anterior coelom of the left side ; 5 mouth ; 6 left posterior coelom ; 7 anus ; 8 right posterior coelom ; 9 right hydrocoel ; 10 left hydrocoel.

We now come to a consideration of the so-called **Dipleurula**, a hypothetical form which has been imagined by some zoologists as the bilateral ancestor of all Echinoderms. The structure of this hypothetical animal will be understood at a glance from an inspection of Fig. 116bis, which represents it as seen from the left side with its ventral surface turned towards the substratum. It is a bilaterally symmetrical animal with a preoral lobe (2) carrying a nervous plate (3), a ventral mouth (5), a terminal or ventral anus (7), three coelomic vesicles on each side (4, 10, 6), and two water-pores (1). How has this form been arrived at ?

It is not arrived at by selecting features common to all the free-swimming bilateral larvae (sometimes called *Dipleurula* larvae) of Echinoderms ; but by picking and choosing from among the characters of different larvae those which, according to the preconceived ideas of its authors, the common ancestor might be supposed to have possessed, and adding one or two characters which none of them possess. For instance, the preoral lobe is very small in pluteus larvae, though well developed in bipinnaria and in the larva of Crinoids ; a preoral nervous system has been detected

only in Crinoid and Echino-pluteus larvae, no Echinoderm larva has a right hydrocoel equal in size to the left, and in Crinoids and Holothurians there is no trace of a right hydrocoel at any stage of existence. Lastly, in no normal* Echinoderm does the right hydrocoel ever possess a water-pore. We do not wish to be unduly critical, but we think it not unreasonable to point out that, in the absence of any test which enables us to decide which characters are ancestral and which secondarily acquired, an ancestor constructed by this somewhat one-sided application of the recapitulation theory can have very little value in advancing zoological knowledge. We do not say that this kind of speculation has no value, for it is a source of delight and stimulus to many minds; but we think that it is most important that its value should not be overrated and that it should not be allowed to divert attention from more important and more practicable problems.

To continue the imaginary history of the dipleurula ancestor. The next change is due to its fixation, which is supposed by Bather to have taken place by the right side of its preoral lobe, though the fixation actual occurs in the middle line. This led to the passage of the mouth to the left side and to the establishment of the radiate structure of most organs except the genital and to the shifting and asymmetry of the coelomic sacs. This brings us to the so-called **Pentactaea**.† Now came the divergence into types. The Holothurian type in which the generative organs never acquire a radial arrangement, was the first to separate. In this type the attachment was entirely lost from the whole life history. Next, after the acquisition of radial structure by the gonads, the Asteroids and Echinoids separated off; of these the Echinoids entirely lost their attachment, while the Asteroids appear to have retained it in some if not in all cases (larval attachment, p. 149). Lastly, or perhaps as a continuation of the main stem but little modified, came the Crinoids, in which the attachment is retained. This type further presents the following remarkable feature which may or may not have been primitive; the mouth shifts from the left side to the hind end, where it lies alongside the anus.

Class ASTEROIDEA ‡

Star-shaped or pentagonal forms with the body flattened in the or-anal axis. The arms are not sharply marked off from the disc and have an ambulacral groove from which the tube feet project. The madreporite is on the abactinal surface.

* Brooks and Field have asserted that in bipinnaria a second madreporic pore normally occurs, but this statement has not been confirmed.

† See Lang's *Comparative Anatomy*, Pt. 2, p. 548.

‡ E. W. MacBride, "The development of *Asterina gibbosa*," *Q.J.M.S.*, 38, 1896, p. 339. H. Ludwig, "Asteroidea" in *Bronn's Thierreich*, Leipzig, 1894-8. Id., *Die Seesterne des Mittelmeeres*, Neapel, 1897. S. Goto, Metamorphosis of *Asterias pallida*, etc., *Journ. Coll. Sc. Japan*, 10, 1898, p. 239. Id., Metamorphosis of *Asterina gibbosa*, *ibid.*, 12, 1898, p. 227. W. P. Sladen, "Report on the Asteroidea," *Challenger Reports*, vol. 30, 1889. E. Perrier, "Echinodermes," in *Exped. Sci. du Travailleur et du Talisman*, Paris, 1894, and in *Mission Scient. du Cap Horn*, vol. vi., Paris, 1891. See also works of Ludwig, Cuénot, Hamann, Delage et Hérouard, *loc. cit.*

The form of body varies from that of a pentagonal disc in which the rays are only marked by the angles (Pentagonasteridae, Fig. 117, Pterasteridae, species of *Culcita*), to that of a star (Fig. 139), in which the disc is small and the arms as sharply marked off from it as in the Ophiurids (Brisingidae).

The number of rays varies in living forms from five to forty-five (*Labidiaster*). Five is the most usual number and is especially constant in the discoidal forms and in those with well-developed marginal plates (*Palmipes rosaceus* is exceptional in having eleven and *Culcita tetragona* in having four). Four is sometimes found as an individual variation. The number of rays shows a distinct tendency to increase in families, in which the arms are long, the disc small, and the marginal plates feebly developed (e.g. Brisingidae, Heliasteridae, Asteriidae, Echinasteridae). When there are more than six rays individual variations in their number are fairly common. In *Labidiaster* in which the arms are very numerous, the number of them increases with the growth of the animal; but in most if not all other cases the full number is laid down in the embryo.

The body is usually compressed dorso-ventrally. On the actinal surface, reaching the whole length of the radii and terminating in the centre of the disc in the oral area or depression, are the ambulacral grooves, and from them project the two, more rarely four, rows of tube-feet. The mouth is placed on the actinal surface in the centre of the disc in the oral depression. There are no circumoral tentacles or tentacular prolongations of any kind round the mouth, but at the distal end of each ambulacral groove there is a red pigment spot which is called the eye or ocellus and over which projects an unpaired tentacle-like structure; this is the ocular tentacle and contains the end of the radial water-vascular trunk. The dermal skeleton is well developed, and carries, especially on the abactinal surface, numerous spines and usually pedicellariae. The anus, which is absent in the Astropectinidae and probably in the Porcellanasteridae, is on

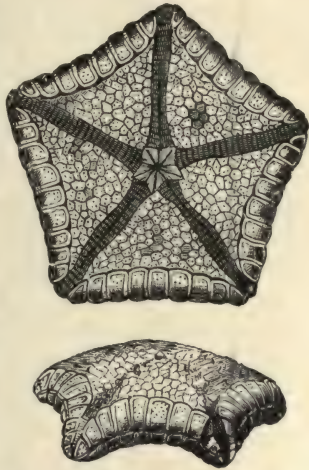


FIG. 117. — *Pentagonaster Parkinson*. Forbes (after Perrier). Seen from below and from the side.

the abactinal surface of the disc in interradius I. II, very nearly, but not quite, at the central point (Fig. 83).

The flattening of the body is carried furthest in *Palmipes membranaceus*, which has the form of a pentagonal sheet of cardboard. While the oral surface is generally flat, the aboral surface is often arched, sometimes considerably so (*Pteraster*, *Hymenaster*, *Marginaster*, *Pentaceros*, *Culcita*, many *Solasteridae*

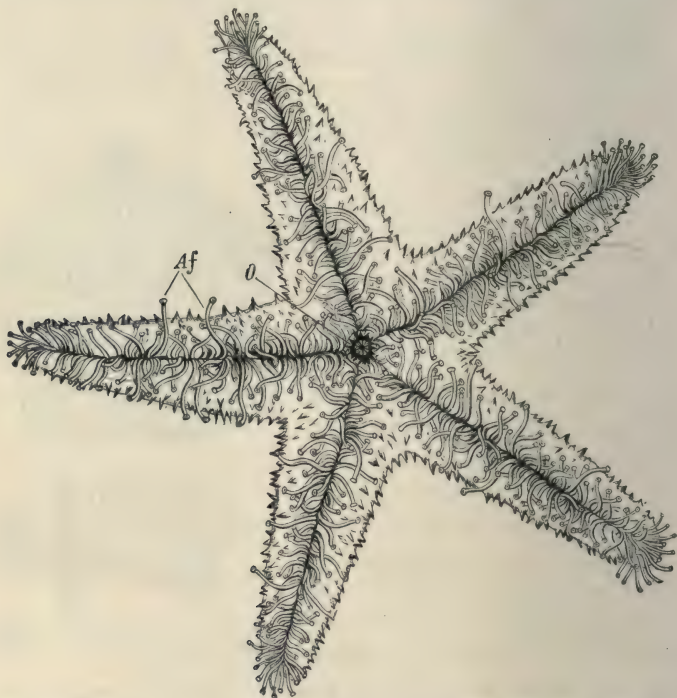


FIG. 118.—*Echinaster sentus* from the oral surface (after A. Agassiz). O mouth, Af ambulacral feet.

and *Asteriidae*). The rays are usually approximately equal in size; inequality generally implies recent mutilation and regeneration.

Starfishes vary in size from those with an arm-radius (centre of disc to extremity of ray), of 1 cm. or less (*Marginaster pentagonus*, .3 cm.) to those in which the same dimension measures 45 centimetres (*Luidia savignyi* to 37 cm., *Freyella remex* to 45 cm.).

The **body-wall** consists (1) of a single layer of ciliated columnar ectoderm, with a cuticle on the outer side and a basement membrane on the inner; (2) of a dermis formed of a gelatinous matrix containing fibrillar connective tissue and calcareous plates and muscular elements; (3) of a layer of ciliated peritoneal epithelium which lines the body cavity. In the ectoderm are sense-cells and gland-cells, and in some parts of the body nerve-fibres and nerve-cells are present in the deeper parts of the same layer.

The integument is more or less hard and stiff owing to the presence of the calcareous plates. These structures may be regularly arranged and in contact with each other, or they may be irregularly disposed rods forming a kind of loose network, through the variously shaped meshes of which such delicate processes of the body-spaces as the tube-feet and dermal branchiae project, or they may be isolated from one another. The calcareous plates may be deeply imbedded in the dermis and not visible from the exterior, or they may lie just beneath the epidermis, so that their shape is more or less completely discernible in surface view. As a general rule some or all of the dermal plates bear granules, or processes and spines of various shapes, or pedicellariae. When these structures project from the surface, as they generally do, the skin has a rough or even spiny appearance; but sometimes, especially when the plates lie deep, they project but little in the fresh state, and the skin is nearly smooth; though even here, in dried specimens, the skin is rough and the spines are discernible from the surface (e.g. *Tylaster willei*, *Porania*, *Culcita*).

In addition to these skeletal structures of the general integument, small calcareous pieces are found in the walls of the tube-feet.

The skeleton of the plates or ossicles falls under two heads, (a) the ambulacral, (b) the ambital.

(a) The **ambulacral skeleton** consists of the ambulacral and adambulacral ossicles, together constituting four rows of plates in each ray (Fig. 119). They form the roof and sides of the ambulacral groove (Fig. 121). The ambulacral ossicles (Fig. 119, *A*) are two rows of rod-shaped structures which meet and are articulated together in the middle line above (Fig. 121), and diverge from one another on each side, abutting at their outer ends upon the adambulacral ossicles (*A'*). These, which correspond in number with the ambulacral ossicles, though they usually alternate with them in position (Fig. 119), form the edges of the ambulacral grooves and carry

the adambulacral spines (Fig. 121, 8). The ambulacral ossicles are always without any form of spinous appendage, and the tubes connecting the

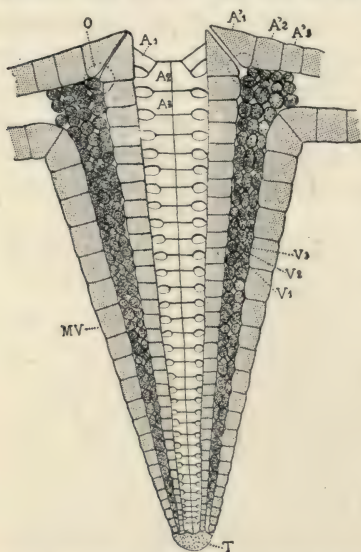


FIG. 119.—Diagram showing the skeletal pieces of the arm of a starfish with adambulacral peristom and biseriate tube-feet, when viewed from the actinal surface (from Ludwig). *A1*, *A2*, etc., first, second, etc., ambulacral ossicle; *A'1*, *A'2*, *A'3*, first, second, third adambulacral ossicle; *O* inner intermediate piece (oral plate); *MV* inframarginal plates; *T* terminal plate; *V1*, *V2*, *V3* ventrolateral plates.

The *superambulacral pieces*, which may be mentioned here, are internally placed and connect the ambulacral ossicles with the marginal plates (Fig. 121, 5); they are found in the *Astropectinidae*, many species of *Linckiidae*, and in some species of the *Porcellanasteridae* and *Archasteridae*.

The first two ambulacral ossicles of each side are more or less fused with one another (they are represented separate in the diagram) and form with the first of the adambulacral series the dental apparatus of the peristom. When the adambulacral pieces of this system are more prominent than the ambulacral, and form the *buccal angles*, the peristom is called *adambulacral* (Fig. 119); when, on the other hand, the ambulacral pieces are the more prominent and the buccal angles are less

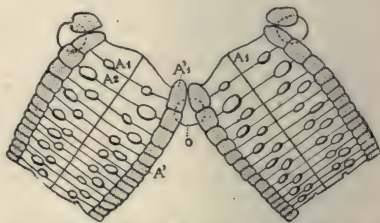


FIG. 120.—Diagram showing skeletal pieces of the proximal part of the arm of a starfish with ambulacral peristom and quadriseriate tube-feet (from Ludwig). *A1*, *A2*, etc., first, second, etc., ambulacral ossicle; *A'1*, *A'2*, *A'3*, first, second, third adambulacral ossicle; *o* inner intermediate piece (oral plate).

developed, we get the *ambulacral peristom* (Fig. 120). Whatever may be the condition in the adult, all young starfishes begin by possessing an ambulacral peristom. The adambulacral pieces of the peristom carry spines.

The **terminal plates** may be mentioned here. They belong to the actinal surface, and one of them is found at the end of each arm on the abactinal side of the last ambulacral ossicles (Fig. 119 *T*). They are especially conspicuous and important when the skeletal plates are first making their appearance; and it can then be seen that they are laid down round the left coelomic sac, i.e. on the actinal surface of the future starfish (p. 147).

(b) The **ambital skeletal**. The rest of the skeletal plates are classified as ambital. They consist of the interambulacral plates and the antambulacral.

The *interambulacral plates* are of three kinds:

(1) the inner intermediate pieces (*o*, Fig. 119), of which there is one in each interradius; they lie on the abactinal side of the two adambulacral pieces which form the buccal angles; (2) the ventrolateral plates, which lie between the adambulacral and the inferior marginals (*V*, Fig. 119); the ventro-lateral plates are often only found on the interradiial portions of the actinal surface of the disc; (3) the inferior marginals, which constitute a row of plates placed at the edge of the arm, just external to the ventro-laterals (Fig. 119, *MV*).

The *antambulacral plates* (Fig. 122) constitute the bulk of the ambital skeleton. They consist of (1) the superior marginals (*M*), which may either be in contact with the inferior marginals or separated by intercalated plates; (2) the eleven primary plates of the apical system, viz. five radial (*R*), five interradiial (*JR*), and one central (*C*); (3) the secondary radial plates of the arms and disc (*Rb* and *Rd*) (*carinalia* of Perrier, *medioradials* of Sladen); these are often not distinguishable in adults from the other antambulacral plates, e.g. many Archasteridae, Porcellanasteridae, Asteriidae, Solasteridae, Echinasteridae; (4) the dorsolateral plates (*dl*), corresponding to the ventro-laterals of the interambulacral skeleton; (5) the supplementary plates of the arms and disc (*s*) which may effect the connexion of the dorsolaterals into a meshwork (hence *reticularia* of Perrier); (6) the madreporic plate (*Md*) placed in the left anterior interradius (the mouth being downward, and the anal interradius forward); the madreporic plate may be either the interradiial plate of the apical system (*JR*, *MD*), or it may be outside this plate (*Md*), or it may be fused with it (*Md*¹).

The primary plates of the apical system are quite distinct in the young starfish, but in later growth are only rarely distinguishable by size or form (some Asterinidae and Pentacerotidae, many Pentagonasteridae) from

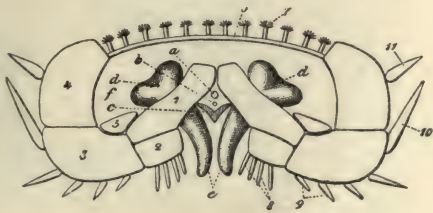


FIG. 121.—Diagram of a transverse section through the arm of *Astropecten*, the hepatic diverticula being omitted. 1 ambulacral, 2 adambulacral ossicle; 3 lower, 4 upper marginal plate; 5 superambulacral ossicle; 6 integument of abactinal surface; 7 paxilli; 8 adambulacral spines; 9 spines of the lower side of the inframarginal plate; 10 lower, 11 upper marginal spine; *a* radial water-vascular vessel; *b* so-called radial blood-vessel; *c* radial nerve; *d* ampulla of tube-foot; *e* tube-foot; *f* perivisceral cavity of arm.

the other plates of the antambulacral surface. Sometimes they remain throughout life as the sole plates of the antambulacral system (*Cnemidaster wyvillei*), and sometimes only a few other plates are developed between them (*Neomorphaster talismani*, *Korethraster setosus*, different species of *Marginaster*).

The dorsolaterals may be connected into an irregular network, and fit closely into one another, and when the marginals are not distinctly developed they pass gradually into the ventrolaterals at the sides of the arms.

The external skeletal structures are spines, spinelets, scales, granules and pedicellariae. Like the plates they are dermal structures and are covered by a layer of ectoderm. They are processes of or movably attached to the subjacent skeletal plates.

The spines are elongated pointed rods, which project, usually singly, from the subjacent plates, to which they are attached by muscles and often by a ligament. They are found mainly on the larger plates of the abactinal surface and on the marginal plates. The spinelets are simply small spines. They often occur in tuft-like aggregations. Sometimes the plates carry-

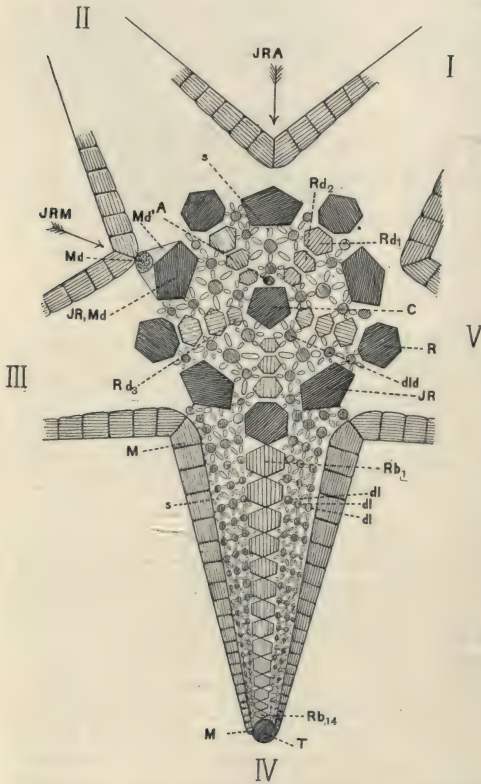


FIG. 122.—Diagram of a starfish viewed from the abactinal side to show the antambulacral skeleton (after Ludwig). The arms are numbered i-v (see Fig. 83). A anus; C central plate; dl dorso-lateral plates of arms; dld ditto of disc; JR interradial plate of apical system; JRA inter-radius in which the anus is placed; JRM interradius containing the madreporite; JR, Md madreporite and interradial as one and the same plate; M marginal; Md madreporite separate from the interradial; Md' madreporite as fused with the interradial; R radial; Rb1, etc. secondary radials of arms; Rd1, etc. secondary radials of disc; s supplementary plates; T terminal plate.

ing such tufts project in a column-like manner; such projecting columns with their tufts of spines are called **paxilli*** (Fig. 121). The spinelets are found principally upon the adambulacral plates and upon the actinal and abactinal intermediate plates; they are attached to the subjacent

* For a somewhat similar arrangement of spines in the Solasteridae and Pterasteridae, see p. 191.

plates by muscles and are covered with a glandular and nervous epidermis. The **scales** are flattened spinelets. The **granules** are short rounded spinelets; they occur set closely together on the skeletal plates.

The **pedicellariae** are pincer-like calcareous structures consisting of two, rarely three, blades articulated to a plate in the dermis, and capable of executing snapping movements by means of a special set of muscles attached to their base. They are contained in the dermis and are covered

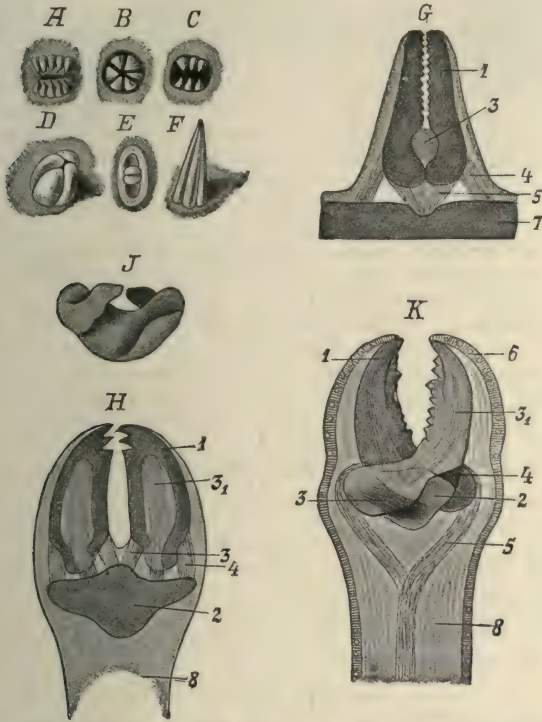


FIG. 123.—Pedicellariae of Asteroids (from Lang). *A-F* grouped spines resembling pedicellariae. *G* sessile pedicellaria of *Gymnasteria carinifera* (after Cuénot). *H* stalked straight pedicellaria, diagrammatic (after Cuénot). *J* basal piece of a stalked crossed pedicellaria of *Asterias rubens* (after Perrier). *K* stalked crossed pedicellaria of *Asterias glacialis* (after Cuénot). 1 calcareous blade of forceps; 2 basal piece; 3 occlusor muscle; 3 axial muscle of the blades attached to the basilar piece and acting as an occlusor muscle; 4 opening muscle; 5 axial band; in *K* this band divides, each branch being inserted into the base of one of the blades in such a way as to strengthen the grip when the pedicellaria is pulled; 6 ectoderm; 7 body wall; 8 stem.

by ectoderm. They may attain a size of 4 mm., but are usually much smaller. They are modified spines, and sometimes small groups of spines are so associated that they can be moved towards one another and act like pedicellariae (Fig. 123, *A-F*). Pedicellariae are entirely absent in the genera *Solaster*, *Echinaster*, *Cribrella*, *Mithrodia*, *Ophidiaster*, *Scytaster*, *Astropecten*.

Pedicellariae are of two kinds, sessile and stalked. **Sessile pedicellariae** (Fig. 123, *G*) arise direct from the integument, to one of the plates of which

they are attached. **Stalked pedicellariae** are at the end of a short soft stalk, the blades articulating with a calcareous piece at the end of the stalk (Fig. 123, *H* and *K*, 2). Stalked pedicellariae are either straight (**forficiform**) or crossed (**forcipiform**) (Fig. 123, *H* and *K*). In the forcipiform pedicellariae the blades cross at their lower ends. Three-bladed pedicellariae constructed after the fashion of the straight variety are occasionally found. The blades of pedicellariae may be longer than they are broad, in which case they are said to be **forcipate**; or they may be broader than they are long, in which case they are **valvulate** (Fig. 124). Valvulate pedicellariae are always sessile.

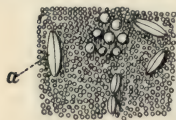


FIG. 124.—Valvulate pedicellariae of *Culcita grex* (after Perrier). *a* one of the five pedicellariae shown in the figure.

Alveolate pedicellariae are sessile pedicellariae in which the blades are inserted into a depression or alveolus in the calcareous plate. Stalked pedicellariae are confined to the Brisingidae, Pedicellasteridae, Heliasteridae, Asteriidae, Zoroasteridae, Stichasteridae, which are united together by Perrier as *Forcipulata*.

Spines are movable: those at the edges of the ambulacral grooves can be bent over the groove. Pedicellariae are no doubt related to such movable spines. However this may be, it is highly probable that they are defensive weapons, seizing and damaging other organisms which come in contact with them, and that they also serve for keeping the skin clear of foreign growths (see the account of pedicellariae under Echinoidea).

The starfishes have some power of bending their arms and the tips are generally turned upwards so as to expose the eye to the light.

Muscles of the body wall. Muscular fibres are found in the inner parts of the dermis near the peritoneum on the dorsal and lateral parts of the arm and disc. They are arranged in an inner longitudinal and outer circular layer. Some of the fibres of the circular layer pass outwards to be inserted into the calcareous plates. The longitudinal layer is specially thickened on the abactinal side of the arms and disc to form a kind of longitudinal muscular band. These bands unite at a central point in the disc.

Skeletal muscles. Special muscles passing between various parts of the skeletal system are present. The most important are: (1) Muscles of the spines and pedicellariae, (2) muscles which pass between the two ambulacral ossicles of a pair, (3) muscles which connect the successive ambulacral ossicles.

All three parts of the **central nervous system** are present, viz. the superficial, the apical and the deep oral (Fig. 125 and p. 123). The ectoneural tracts consist of a circumoral ring and of radial

nerve trunks, the whole lying in the deeper parts of the ectoderm. It is in connexion with a diffuse ectoneural plexus found throughout the ectoderm, and at the mouth with an endoneural plexus. The apical or mesoneural nervous system and the deep oral system have already been sufficiently described (p. 123).

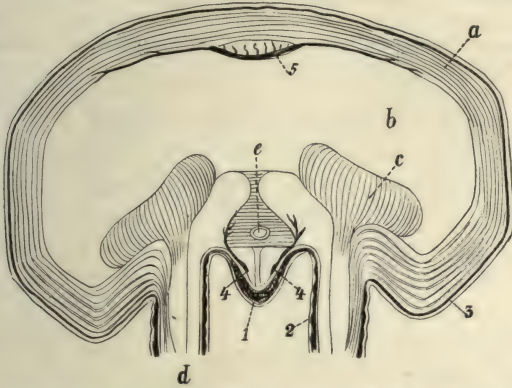


FIG. 125.—Scheme of the nervous system of the arm of a starfish (after Cuénot). *a* wall, *b* body-cavity of arm; *c* ampulla of tube-foot; *d* tube-foot; *e* radial canal of water-vascular system; *1* radial portion of ectoneural central nervous system; *2* ectoneural plexus of tube-foot; *3* ectoneural plexus of skin; *4* Lange's nerve cords (deep oral); *5* mesoneural plexus just beneath the longitudinal muscle.

The structure of the ectoneural plexus and its relation to the ectoderm are best seen by examining the annular (circumoral) nerve ring or the radial prolongations of it. The ectoderm here is much thickened and consists of elongated columnar cells with their nuclei near their outer ends; the inner ends of the majority of the cells, which may be called supporting cells, taper and form a supporting tissue for a plexus of fine nerve fibres and scattered ganglion cells, which are here especially conspicuous and cause the thickening of the ectoderm. Some of the ectoderm cells are sense cells, and their inner ends do not form supporting fibres but branch out and join the nervous plexus. There are special aggregations of these round the ends of the tube-feet. The ectoderm along these central concentrations of the ectoneural system is much thickened, and its cells contain yellow pigment grains which give the whole tract—in both its annular and radial portions—the appearance of a yellow streak.

At the ends of the arms, this thickened tract of nervous ectoderm is continued over the terminal tentacle-like process (ocular tentacle), which forms the projecting end of the radial water-vascular trunk.

The eye is on the oral side of the base of this tentacle; it is coloured bright red and formed by a special thickening of the radial nerve tract



FIG. 126.—*Astropecten aurantiacus*, end of ray with the eye *Oc* surrounded by spicules (from Claus, after Haeckel).

and subjacent connective tissue. In a typical case* each eye consists of a number (50 to more than 100) of funnel-shaped ectodermal pits, the cells of which contain the red pigment and end in a clear highly-refractile rod which projects into the cavity of the pit. The pit is closed towards the exterior by the cuticle, which may have on its inner side a lens-like thickening. The pigment cells are continued internally as fine fibres which join the nervous tissue of the radial nerve. The pits increase in number with the growth of the animal and they appear to contain a transparent gelatinous tissue. In some cases there are no pits and the pigment cells are distributed uniformly over the surface of the ocular cushion (*Astropecten pentacanthus, mülleri*).

The alimentary canal begins with a mouth which is placed in the centre of the actinal surface of the disc in the buccal membrane, and leads into a short oesophagus or directly into the spacious stomach (Figs. 127, 132). The oesophagus passes quite gradually into the stomach from the abactinal part of

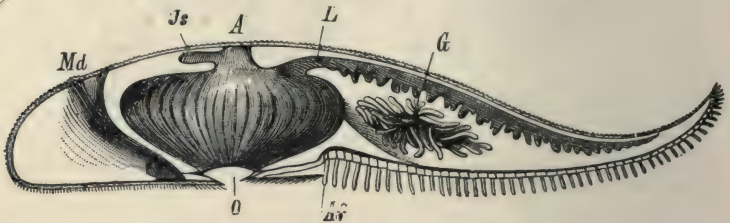


FIG. 127.—Longitudinal section through the disc and an arm of *Solaster endeca* (from Claus, modified after G. O. Sars). *O* mouth leading directly into the wide stomach; *A* anus; *L* hepatic diverticulum of the stomach; *G* gonad; *Md* madreporite; *Js* rectal caecum; *Af* tube-foot.

which two caecal diverticula (hepatic) are given off into each arm. From the stomach a short rectum, which receives the rectal caeca, leads to the anus, which opens on the abactinal surface in interradius *I. II* (Figs. 83, 122).

The buccal membrane is the part of the body-wall round the mouth in the oral depression and is devoid of calcareous structures; the circular muscular fibres in it act as a constrictor and the longitudinal as dilators of the mouth opening. The oesophagus passes without any line of demarcation into the stomach; it is beset with ten glandular diverticula in *Echinaster* and *Cribrella*. The stomach is a spacious, thin-walled sac, divided by a horizontal fold (absent in the *Astropectinidae* without an anus) into an oral (cardiac) and aboral portion (pyloric sac). Its walls are often considerably folded, so that it appears lobed. From its aboral portion the stomach gives off the hepatic or pyloric caeca (Fig. 128), one pair into each arm. These are tubular structures beset with numerous

* Pfeffer, *Zool. Jahrb. Anat.*, 14, 1901, p. 523.

secondary and tertiary glandular diverticula, and suspended to the abactinal body-wall of the arm by two mesenteries (Fig. 129, 24). The two caeca of a pair usually arise separately from the pyloric sac, but in some cases (*Asterias*, etc.) they are united near the stomach and arise from it by a common tube. The proximal end of each of these caeca gives off on its actinal side a pouch, called *Tiedemann's pouch* (specially developed in the Echinasteridae and Asterinidae). The abactinal side of the stomach is closely applied to the body wall, but between the two is a variable number of interradially placed glandular diverticula: these are the **rectal caeca** (Fig. 127, *Js*). They vary considerably in form, size and number (from two to five, in *Luidia* they are absent), and they open into the rectum except in the *Astropectinidae*, in which the rectum and anus are absent and the caeca open directly into the stomach. The **rectum** is a short tube which leads from the stomach to the anus. The **anus** (p. 167) is absent in the *Astropectinidae* and *Porcellanasteridae*. The alimentary canal is lined throughout by a glandular ciliated epithelium, and, in some forms at least, a few calcareous bodies are found (*Culcita*, *Ophidiaster chinensis*) both in its walls and in the mesenteries which attach it to the body-wall.

The **mesenterial attachments** of the alimentary canal are as follows: (1) a pair of muscular strands run from the oral wall of the stomach in each radius to be inserted along the ambulacral ossicles of the ray (Fig. 132, *ret*); they serve to retract the stomach when it has been evaginated for the prehension of food; (2) a number of fine cords passing from the aboral wall of the stomach to the body-wall (Fig. 132, *mes*); these are remains of the septum between the right and left posterior coeloms of the larva; (3) the mesenteries of the hepatic caeca (p. 177 and Fig. 129, 24); these fuse with one another distally, but proximally end freely so that the space between them is in open communication with the general body-cavity. They are probably remains of the mesentery which separated the right and left posterior body-cavities of the larva. On this view the spaces between the two mesenteries of a pair are parts of the right posterior body-cavity, and, if the division between the two body-cavities were retained in the adult, the two mesenteries of one caecum should join respectively the mesenteries of the caeca on each side of it in the disc, so as to cut off just above the stomach a circular patch of body-cavity with two prolongations into each arm. (4) Two bands which pass from the aboral end of the wall of the axial sinus to the stomach. These were formerly supposed to be processes of the aboral sinus.



FIG. 128.—*Asterina gibbosa* with the abactinal body-wall removed (from Claus). *Ld* hepatic caecum *G* gonad.

The **coelom**. The relations and development of the coelom have been more fully elucidated in Asteroids than in any other class of Echinodermata. It represents the following parts : * (1) the general or perivisceral body-cavity, (2) the axial sinus and inner circumoral periaermal ring, (3) the so-called outer circumoral periaermal ring with its radial prolongations between

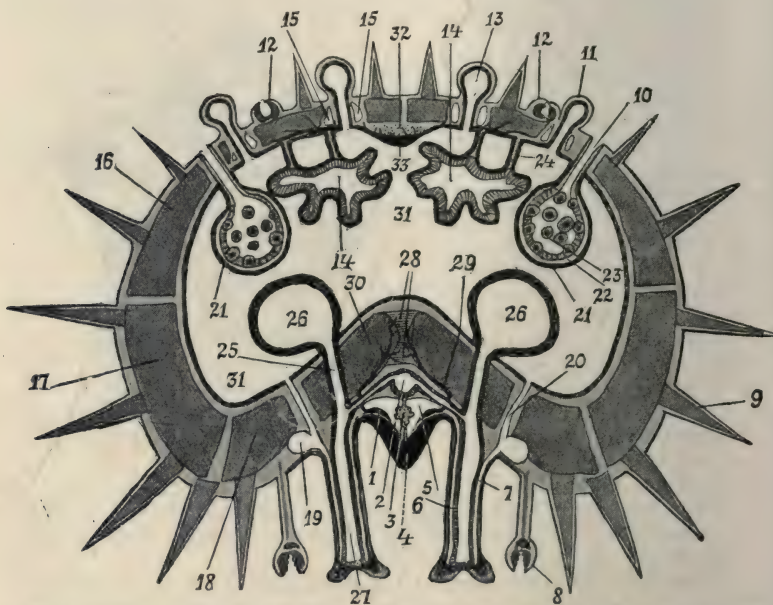


FIG. 129.—Diagrammatic view of a transverse section through the arm of an Asteroid (from Lang). 1 trunks of the deep oral nervous system (Lange's nerves); 2 radial water-vascular trunk; 3 tissue of so-called radial blood-vessel; 4 radial nerve of the superficial oral system; 5 radial periaermal canal; 6 and 7 branches of the same to the walls of the tube-feet; 8 stalked pedicellaria; 9 spine; 10 genital aperture; 11 papula with contained body cavity; 12 sessile pedicellaria; 14 hepatic caecum; 15 peribranchial cavity; 16 supra-marginal; 17 inframarginal; 18 adambulacral plate; 19 marginal canal communicating at 20 with the perivisceral coelom; 21 peritoneal epithelium; 22 genital sinus; 23 gonad; 24 mesenteries of hepatic diverticula; 25 tube connecting tube-foot with 26 ampulla; 27 cavity of tube-foot; 28 upper and lower transverse muscles connecting the ambulacral plates; 29 branches of the deep oral nerve trunks; 30 ambulacral plates; 31 perivisceral cavity; 32 longitudinal muscle; 33 apical nervous system.

the ambulacral nerves and the radial water-vascular trunks, (4) the aboral sinus surrounding the generative rachis and the sinuses in the walls of the gonads, (5) the water-vascular system, and (6) the gonads.

The general body-cavity which is derived from the right and

* For the general relations and development of these structures the reader is referred to p. 126 et seq. and p. 142 et seq.

left posterior body-cavities of the larva is a perivisceral space in relation with the stomach, rectum and pyloric caeca: it is a continuous space, is found in the disc and in the arms on the abactinal side of the ambulacral ossicles and is traversed by certain mesenteries which have already (p. 177) been described. It is lined by a ciliated epithelium, and contains an albuminous fluid with floating amoeboid cells.

The **papulae** or dermal branchiae (Fig. 129, 13) are thin projections of the body-wall found principally on the abactinal surface of the disc and arms and containing prolongations of the perivisceral cavity. Round the bases of the papulae there is generally present in the body-wall a space lined by an epithelium and supposed to be developed as a diverticulum of the perivisceral cavity. These

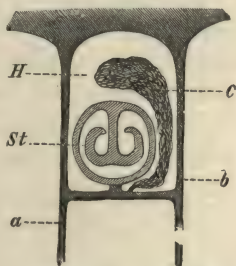


FIG. 130. — Diagrammatic transverse section through the axial sinus of a starfish (from Ludwig). *a, b* the lamellae of the inter-brachial septum; *C* axial organ; *St* stone-canal; *H* axial sinus. The upper side of the section is the body-wall side.

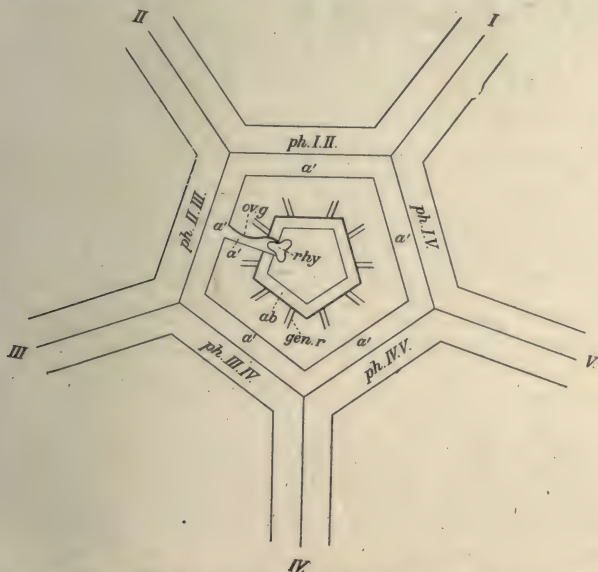


FIG. 131.—Diagram showing the arrangement of the periaermal spaces, etc., of a starfish, seen from the aboral side (after MacBride). *a'* axial sinus and inner periaermal ring; *ab* aboral circular sinus; *gen.r* generative rachis; *ov.g* axial organ; *ph.I.II . . . ph.IV.V* the five parts of the so-called outer periaermal ring; *rhy* vestige of right hydrocoel; *I-V* the arms numbered.

spaces are called the peribranchial cavities (Fig. 129, 15, Fig. 132, *pbr*).

The **axial sinus** is a tube passing from the abactinal to the actinal surface in the interradius of the madreporite (Fig. 132, *ax.s*). It is contained in an interbranchial septum (Fig. 130) and is lined by a ciliated epithelium. The stone-canal and axial organ project into it, being attached to its inner wall, i.e. to its wall next the oro-anal axis, by membranes (*st.c*). Orally the

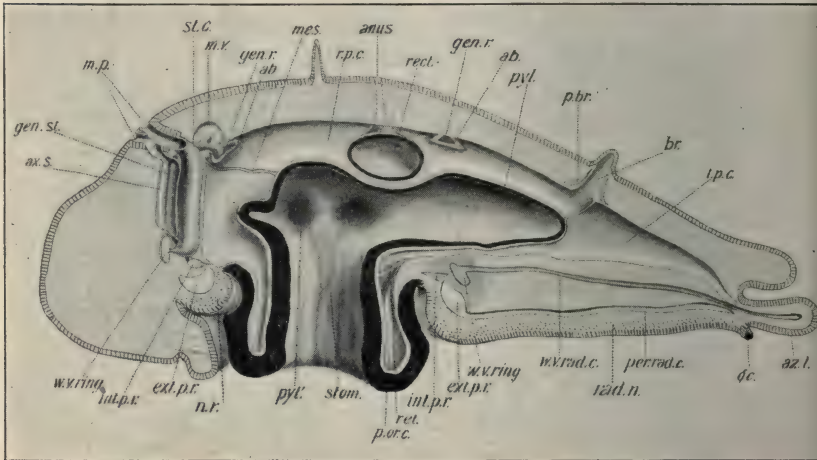


FIG. 132.—Longitudinal vertical section through the disc and one arm of a young starfish (after an original drawing by Prof. E. W. MacBride, F.R.S.). The section passes through the interradius of the stone-canal and madreporite. *ab* aboral sinus; *ax.s* axial sinus; *az.l* terminal unpaired tentacle; *br* papula (dermal gill); *ext.p.r* external peribranchial space; *gen.r* genital rachis; *gen.st* genital stolon (prolongation of rachis into axial organ); *int.p.r* internal peribranchial space; *l.p.c* left posterior coelom of larva, hypogastric coelom of adult; *mes* remains of the mesentery separating the left posterior (hypogastric) and right posterior (epigastric) coeloms; *mp* madreporic pores; *m.v* madreporic vesicle (right hydrocoel); *nr* nerve ring; *oc* eye; *pbr* peribranchial space; *perrad.c* radial peribranchial canal; *p.or.c* perioral coelom, an outgrowth of the hypogastric coelom, from its walls are formed the retractors of the stomach; *pyl* pyloric sac; *pyl'* the opening of a pyloric caecum; *rad.n* radial nerve; *rect* rectum; *ret* retractor of the stomach; *r.p.c* right posterior coelom (epigastric of the adult); *st.c* stone-canal; *stom* stomach; *tf* tube-foot; *w.v.rad.c* water-vascular radial canal; *w.v.ring* water-vascular ring canal.

axial sinus is continuous with the so-called inner peribranchial space which surrounds the mouth (Fig. 131, *a*¹, Fig. 132, *int.pr*). At its aboral end it communicates with the stone-canal on the one hand and with the exterior through some of the pores of the madreporite on the other (Fig. 132, *mp*). The axial sinus is derived from the anterior body-cavity of the larva.

The outer circumoral peribranchial ring, which is separated by a slightly oblique septum from the inner peribranchial ring just described, is not really a ring at all. It is (Fig. 131, *ph. I. II.* etc.)

made up of as many interradial pieces as there are arms, each piece being prolonged into two adjacent arms. It thus comes about that each arm has a prolongation of two pieces of the so-called outer periaemal ring, the septum between these two radial prolongations being the septum (Fig. 129, 3) which divides the radial periaemal canal into two parts and in which the so-called radial blood-vessel runs. This outer circumoral periaemal ring is derived for the most part from the left posterior body-cavity of the larva (see p. 145). It is lined by a flat epithelium, whether ciliated or not is unknown.

There is said to be a canal in the body-wall at the edge of the ambulacral groove which communicates at intervals with the radial periaemal space and with the perivisceral cavity (Fig. 129, 19).

The **aboral sinus** (Figs. 131 and 132 *ab*) is a circular or pentagonal sinus placed on the aboral side of the stomach between it and the skin, and giving off in each interradius two prolongations * to the generative organs (*gen.r.*). In this sinus and its prolongations lies a peculiar cord of tissue, consisting partly of generative rachis and partly of vascular tissue. The space, formerly supposed to be a blood-vessel, in the wall of the gonads, is developed as a part of this system, but in the adult there is a septum which shuts it off from the rest. The whole of the aboral sinus with its prolongation to the gonads and the sinus in the walls of the latter is developed as a part of the left posterior body cavity of the larva.

The **water-vascular system** is lined throughout by a ciliated epithelium, has thin muscular walls, and contains a colourless albuminous fluid in which float amoeboid cells. It consists of a circumoral vessel, which is placed on the inner side of the buccal membrane close to the calcareous pieces of the peristome, sends prolongations—the radial vessels—into the radii, and communicates with the exterior through the stone-canal and axial sinus. The stone-canal passes aboralwards in interradius *II. III* (the so-called left anterior). At its aboral end it opens into the axial sinus on the one hand and to the exterior through the pores of the madreporite on the other. The madreporite is

* The two cords which pass from the point where the axial sinus abuts upon the aboral sinus to the stomach are not processes of the generative rachis and aboral sinus as was formerly supposed, but of the wall of the axial sinus (see p. 177).

a calcareous sieve-like plate perforated by many pores—the secondary water-pores. Though in the adult most of the pores of the madreporite lead directly into the stone-canal, some of them open into the axial sinus. In the larva the primary water-pore opens into the axial sinus. With later growth this one pore becomes divided by folding into many, the epithelium

of some of which becomes directly continuous with the epithelium of the stone-canal, but some of the pores retain their direct connexion with the axial sinus.

The circumoral vessel bears two kinds of appendages—the polian vesicles (p. 184) and Tiedemann's bodies (p. 185). The radial canals, which lie between the heads of the ambulacral ossicles in the angle formed by their apposition (Fig. 129), give off on each side as many lateral branches as there are tube-feet. Each of these branches goes to a tube-foot and is connected by a canal which passes between two adjacent ossicles, with the internally placed ampulla. In some forms there are two ampullae to each tube-foot (many *Astropectinidae*). The

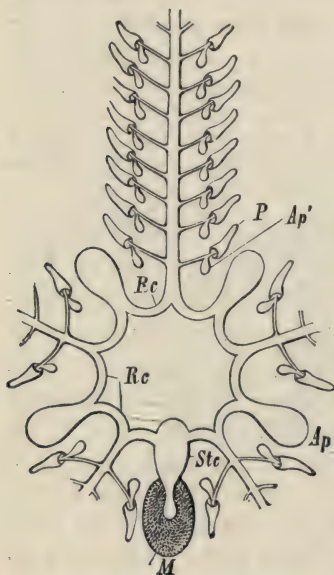


FIG. 133.—Diagrammatic representation of the water-vascular system of a starfish (from Claus). *Ec* circumoral vessel; *Ap* polian vesicle; *Stc* stone-canal; *M* madreporite; *P* tube-feet; *Ap'* ampullae of the same.

radial canals end blindly at the end of the arm in the ocular tentacle.

The tube-feet are always pointed in the young, but in the adult they often terminate in suction-like expansions. Sometimes the distal feet of an arm are pointed and the proximal suction-like. The pointed feet are tactile, while the others are adhesive as well. The tube-feet have a well-developed ectoneural nerve layer, and longitudinal muscles only, except in the sucking disc where there are radial fibres, the contraction of which brings about the adhesion of the disc. At the junction of the lateral branches with the radial trunk there is a valve

which prevents the fluid passing back into the radial canal, so that when the ampulla contracts, it drives its contents into and so extends the tube-foot. The retraction of the foot is caused by the contraction of the longitudinal muscles of its walls, the fluid being driven back into the ampulla. If the tube-foot has a sucker, it is able to be attached to external objects and then by its contraction to draw the body of the starfish towards the object. Of course movement of the body in this way can only be effected when a number of feet are acting together in a co-ordinated manner. If a starfish be removed violently from its substratum, the attached sucker will be broken off and left on the stone and water will be ejected from the lacerated ends of the contracting tube-feet.



FIG. 134.—Diagrams of transverse sections through the stone-canals of various Asteroids (after Lang). 1 membrane by which the stone-canal is attached to the wall of the axial sinus; 2 epithelium of the axial sinus; 3 epithelium of stone-canal; 4 connective tissue of wall of stone-canal.

The stone-canal projects into the axial sinus (p. 180). On one side of it, viz. on the side opposite that by which it is attached to the wall of the axial sinus (Fig. 130), there is a longitudinally disposed fold of its lining membrane. In the simplest cases this fold projects into the canal as a ridge (*Echinaster purpureus*, *Brisinga coronata* (Fig. 134, A). In other forms (*Asterina gibbosa* Penn., *Cribrella oculata* Linck, etc.) the free edge of the fold splits into two lamellae (Fig. 134, B), which in yet other species (of *Asterias*, *Pentaceros*, *Gymnasteria*, etc.) become coiled (C). A further complication is introduced by the fusion of the ridge with the opposite wall of the canal and the formation, from each surface of the septum so constituted, of a spirally coiled lamella (species of *Astropecten*, etc., D). Finally there are forms (*Astropecten aurantiacus*, species of *Luidia* and *Culcita*) in which these septa are present in great number and divide the whole lumen into many irregular chambers. All these ridges and lamellae vanish at the lower end of the canal, where it joins the circular vessel. The walls of the stone-canal and the lamellae, etc., which project into it, contain a strong deposit of calcareous matter.

The small sac beneath the madreporite (Fig. 132, *mv*), sometimes called the ampulla, is the small right hydrocoel (p. 144).

The discovery of the communication between the upper end of the stone-canal and the axial sinus, we owe to the work of Perrier, Durham, and MacBride. The number of madreporites and stone-canals varies considerably. In the majority of cases there is only one of each, but there may be more, and this increase in their number is usually, though not always, associated either with an increase in the number of arms, whether such appears as an individual variation or as a constant specific character, or with the power of asexual reproduction by fission across the disc which some starfishes possess. Though the increase in the number of madreporites is generally associated with a greater number of arms than five, it is by no means always found in such forms. For instance, in the genera *Heliaster* and *Labidiaster* which normally have a large number of arms there is only a single madreporite.

The increase in the number of madreporites is found most frequently in the families Asteriidae, Stichasteridae, Echinasteridae, and Linckiidae, and the following table* in which the abbreviation M is used for madreporite shows some of the most conspicuous instances of it:—

Asterias calamaria Gray, with 6–12, usually 7 arms, has in 7-armed forms usually 1, rarely 2 M; but in a 12-armed specimen 2 M and in an 11-armed one, 4 M have been observed.

Asterias tenuispina Lam., has in 5- to 9-armed forms 1 to 3, rarely 4 M.

Asterias capensis Perr., has 6 (rarely 5) arms and 3 M.

Asterias rubens L., exceptionally 2 M in 5-armed forms.

Stichaster polyplax M.Tr., has 7 arms and 1 to 5, usually 3 M.

Stichaster albus Stimps., has 5 to 7 arms and 1 to 2 M.

Acanthaster echinites Ellis and Solander, has in 13- to 20-armed specimens 5 to 16 M.

Acanthaster ellisii Gray, has with 11 to 19 arms 5 to 15 M.

Echinaster eridanella M.Tr. and *E. purpureus* Gray, have in 5-armed individuals 1 M, in 6- or 7-armed 2 M.

Ophidiaster germani Perr., has in 5-armed forms 2 M.

Linckia multiflora Lam., has often 2 M in 5-armed specimens.

Linckia pacifica Gray, var. *diplax* M. Tr., and *L. guildingii* Gray, have as a rule 2 M in 4- to 7-armed specimens.

In the above instances the madreporites are in different, either contiguous or remote, interradii, but cases are known in which there are two madreporites and canals in the same interradius as an individual variation (*Linckia multiflora* Lam., *Heliaster multiradiata* Gray, and in a 6-armed example of *Asterias glacialis* O.F.M.), and Giard has described a specimen of *Asterias rubens* with one madreporite and two stone-canals passing off from it. Finally it must be mentioned that sometimes the madreporite is divided into several pieces, all however connected with the same stone-canal.

Tiedemann's bodies are small yellowish glandular bodies attached to the inner wall of the circumoral vessel into which they open (Figs. 135, 136). They consist of branching tubes of

* Taken from Ludwig's excellent account in Bronn's Thierreich to which the reader is referred for the facts and literature relating to the variation in the number of madreporites.

cubical ciliated yellow epithelium. There are usually two in each interradius, except that of the madreporite, which has only one, and they are supposed to be of the nature of lymphatic organs and to bud off cells into the water-vascular system.

Like so many other features of Asteroid anatomy the **polian vesicles** vary considerably both in number and arrangement throughout the class, even in closely allied forms. They are large vesicular structures with muscular walls and long stalks which open interradially into the circumoral vessel (Fig. 136). Sometimes (*Asterias rubens* and *glacialis*, etc.) they are absent altogether; sometimes there is one in each interradius, except that

of the madreporite, in which there are none at all or two (species of *Astropecten*); finally there are cases of two, three or four or even more in each interradius; in the latter case it is common to find several vesicles opening by one stalk. It is supposed by some that the polian vesicles are contractile structures acting as central organs to vary the pressure in the whole water-vascular system, by others that they

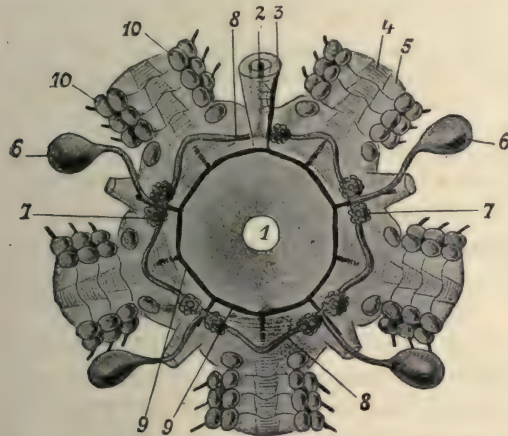


FIG. 136.—Circumoral water-vascular vessel with appendages of *Asterina gibbosa* (after Cuénot, from Lang), seen from the aboral side. 1 mouth in the centre of the buccal membrane; 2 stone canal; 3 axial sinus; 4 transverse muscles of the ambulacral ossicles; 5 ambulacral ossicles; 6 polian vesicles; 7 Tiedemann's bodies; 8 circumoral vessel; 9 ring of supposed vascular tissue; 10 ampullae of tube-feet.

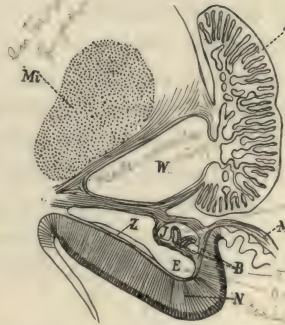


FIG. 135.—Vertical section through an interradial region of the peristome of *Asterias rubens* L. (after Ludwig), showing the connexion of one of Tiedemann's bodies with the water-vascular ring. B tissue of the so-called vascular ring; E outer periaermal ring; J inner periaermal ring; Mi interradian muscle of peristome; Mh buccal membrane; N circumoral nerve-ring; T Tiedemann's body; W water-vascular ring; Z oral portion of deep oral nervous system (Lange's nerve).

are of the nature of lymphatic glands, and that their lining membrane—which has the form of a connective tissue network containing dividing cells in its meshes—buds off amoeboid cells which enter the fluid of the system.

The **axial organ** (ovoid gland, heart) is a fold of the wall of the axial sinus, into which it projects. Its walls are secondarily folded so that it appears in section to contain prolongations of the axial sinus. It consists mainly of connective tissue and of cells derived from a prolongation of the generative rudiment (pp. 131, 146).

The so-called **vaseular system** (lacunar system) of Asteroids consists of tracts of connective tissue in which the fibres are sparser, the ground substance stains more deeply and the leucocytes are more numerous than in the ordinary connective tissue. There is a cord of it in the vertical septum dividing the radial periaermal canal (Fig. 129, 3): this is the so-called radial blood-vessel. This is continuous with a circumoral cord of the same tissue (Fig. 135, B). There is a certain amount of it in the wall of the stomach, which presumably is in connexion with the circumoral tract, and it is possible that the latter may send prolongations on to the axial organ. There is also a tract of it in close association with the generative rachis in the wall of the aboral sinus.

The vascular tissue is sometimes described as consisting of bundles of anastomosing canals without any epithelial lining and containing a coagulable fluid. A definite circulation of this fluid has never been observed.

The sexes are separate. *Asterina gibbosa* however has been said * to be a protandrous hermaphrodite, the same gland producing in young specimens spermatazoa and in old ones ova.

The **generative organs** consist of bunches of tubes which are attached on each side of the interbrachial septa to the abactinal body-wall (Fig. 127). There are therefore twice as many gonads as there are arms. Each gonad consists of one or of several tufts of tubes. In the latter case, the gonads extend into the arms, to the dorso-lateral wall of which they are attached. Each gonad opens to the exterior by one simple opening (rarely subdivided into several) in the abactinal wall of the disc, or, when there are several gonadial tufts, by as many pores as

* Cuénot, L. *Arch. Zool. Exp. et gen.* 5 bis, 1888.

there are tufts, along the sides of the abactinal surface of the proximal parts of the arms. The gonad tubes are lined by a simple epithelium which gives rise to the generative cells, and the external openings are always on the dorsal surface except in *Asterina gibbosa* and *Asterina pancerii* Gasco, in which they open on the actinal surface, no doubt in correspondence with the fact that these animals attach their ova to foreign objects.

The composition of the gonads of a single tuft or of several tufts is often a generic character, but sometimes both conditions are found in the same genus (e.g. *Echinaster*).

The gonads are really the peripheral parts of the **generative rachis**. This structure consists of a cellular cord placed in the wall of the aboral sinus on the dorsal side of the stomach. It gives off a prolongation into the axial organ, and in each inter-radius two cords proceed from it to the gonads. These cords are accompanied by a prolongation of the aboral sinus, which reaches as far as the gonads and surrounds them (p. 181).

Except in those forms in which there are arrangements for the care of the brood, external sexual differences are only occasionally present, and are then usually confined to differences in colour.

A brood pouch is developed on the dorsal surface of the Pterasteridae (see p. 192). In some of the Astropectinidae the eggs pass into the interstices between the stalks of the paxilli and there undergo their development.

In *Stichaster nutrix* Studer describes the young as being at first in outgrowths of the stomach where they undergo their early development, and then as passing on to the edges of the mouth. In *Asterias perrieri* Smith and other species the young are described as being attached to the oral surface of the disc in the neighbourhood of the mouth, and there undergoing their development; the arms being slightly bent over them for protection. In species of *Diplasterias* similar phenomena appear to occur.

They are all marine and crawl upon the bottom of the sea. They capture their food by means of their tube-feet and many of them have the power of partially everting their stomach, the inner surface of which is applied to their prey.

Many of them have the power of autotomously severing their arms from the disc and of regenerating arms so lost. The power of regenerating lost parts is great in all members of the

group, and in some cases it appears that a single arm can reproduce the whole animal. This appears to be the explanation of the so-called comet-forms, which consist of a large arm carrying a small disc with four small arms. Fission of the body through the centre of the disc into two parts sometimes occurs. The power of regeneration possessed by a wounded surface sometimes leads to the production of curious forms, e.g. in *Linckia multifora* the wounded surface of an arm has been described as forming a new disc with four arms.

The development (p. 133) is rarely direct, and the young usually pass through the free-swimming larval stage called *bipinnaria*. Including brachiolaria larvae about twenty bipinnaria larvae are known. Most of these have not been related to their adults. The larva of *Asterina gibbosa* may be regarded as a much modified bipinnaria; it has the power of swimming feebly with the cilia of its larval organ.

Bipinnaria asterigera is the larva of *Luidia sarsii*; it is the largest bipinnaria known (1-1½ cm.). *B. metschnikoffi* and *mülleri* probably belong to species of *Astropecten*. *B. russoi* and *buryi* have been assigned to *Asterias glacialis*.

The *Asteroidea* are found fossil from the Cambrian onwards, but the known fossil forms are not nearly so numerous as in the case of Crinoids and Echinoids. This is doubtless due to the fact that their tissues do not lend themselves so readily to preservation as do those of the above-named classes. The early forms do not differ essentially from those now living. The class is divided into two orders—the *Encrinasteriae*, in which the ambulacral plates alternate on the two sides of the arm and the madreporite is on the lower surface; and the *Euasteriae*, in which the ambulacral plates are opposite one another and the madreporite is on the dorsal surface. The *Encrinasteriae*, are exclusively Palaeozoic, while the *Euasteriae* include all the living forms and make their first appearance in the Silurian.

Order I. ENCRINASTERIAE.

With characters as above.

Aspidosoma Goldf. lower Devonian; *Palaeaster* Hall (*Archasterias* J. Müll), Silurian, Devonian and Carboniferous; *Urasterella* McCoy (*Stenaster* Billings), lower Silurian; *Palasterina* McCoy; *Palaeodiscus* Salter; *Palaeocoma* Salter, upper Silurian; *Salteraster*, etc.

Order II. EUASTERIAE.

With characters as above.

Sub-Order 1. PHANEROZONIA.

With large marginal plates. The supramarginal and inframarginal plates are in contact. Papulae restricted to the abambulacral surface within the area bounded by the supramarginal plates. Ambulacral plates usually broad. Tube-feet in two rows in each arm. Oral adambulacra prominent. Pedicellariae when present sessile.

Fam. 1. **Archasteridae**. Marginal plates thick, with spines or spiniform papillae. Adambulacral plates large and not compressed. Ventrolaterals and marginals with spines or paxilli. Superambulacral plates absent. *Pararchaster* Slad.; *Pontaster* Slad.; *Cheiraster* Studer; *Pectinaster* Perr.; *Lonchotaster*, *Dytaster*, *Plutonaster* Slad.; *Archaster* Müller and Troschel; *Gnathaster* Slad.; *Asterodon* Perr.; *Odontaster* Verrill; *Mimaster* Slad.; *Goniopecten* Perr.; *Leptogonaster* Slad.; *Pseudarchaster*, *Aphroditaster* Slad. British species: *Pontaster tenuispiins*, Scilly, Faeroe Channel, etc. 90–60 fms. *Plutonaster bifrons*, Faeroe Channel, etc., 200–1,300 fms.; *Pl. bifrons*, N. of Ireland, 1,360 fms.

Fam. 2. **Porcellanasteridae**. Marginal plates well developed, but thin and porcellaneous in appearance, and apparently naked or covered only with a thin epidermal layer. Abactinal area covered with membrane and carrying in its centre an epiproctal prominence (Fig. 137). Anus said to be absent. Actinal surface of disc is covered interradially with squamiform plates. Cribriform organs (1 to 14 in each inter-radius) present. Adambulacral plates large with simple marginal armature uniserially disposed. Excepting *Ctenodiscus*



FIG. 137.—*Porcellanaster gracilis* Sladen, side view, showing three cribriform organs and the epiproctal prominence.

all genera are exclusively from the deep sea. Cribriform organs are situated on the marginal plates in the inter-brachial region of the disc, and extend when numerous on to the base of the arms. They consist of a number of parallel vertically arranged calcareous lamellae equal in length to the height of the two series of marginal plates.

Porcellanaster W. Thoms. (Fig. 137); *Styracaster*, *Hyphalaster*, and *Thoracaster* Slad.; *Pseudaster* Perr.; *Ctenodiscus* Müll and Trosch. British species: *Ctenodiscus cristatus*, Faeroe Channel, 312 fms.

Fam. 3. **Astropectinidae**. With large marginals bearing spines or spiniform papillae. Actinal interradiial areas small. Abactinal skeleton with paxilli (Fig. 121). Tube-feet conical. Superambulacral plates present. Anus absent. Pedicellariae rarely present. In *Leptoptychaster kerguelensis* the eggs pass into the spaces between the groups of paxilli and there develop (W. Thomson, J. Lin. Soc. London, 1876, 13).

Craspidaster Slad.; *Leptoptychaster* Smith; *Moiraster* Slad.; *Blakaster* Perr.; *Astropecten* Linck; *Psilaster* Slad.; *Phoxaster* Slad.; *Bathylaster* Dan. and Kor.; *Ilyaster* Dan. and Kor.; *Luidia* Forbes; *Platasterias* Gray. British species: *Leptoptychaster arcticus*, Faeroe Channel, 1,312 fms. *Astropecten irregularis (aurantiacus)* Atl. and Med., 10–1,000

fms. *Luidia ciliaris*, E. N. Atl., to 87 fms., *L. sarsii*, E. N. Atl., to 374 fms.

Fam. 4. **Pentagonasteridae.** Interbranchial region of disc well developed, so the body is pentagonal with more or less concave sides. Marginals well developed. All the plates, both dorsal and ventral, form a close mosaic, and are granular or naked. Anus present, but often hidden by paxilli. *Pentagonaster* Linck. (Fig. 117); *Stephanaster* Ayres; *Astrogonium* M. and T.; *Calliaster* Gray; *Chitonaster* Slad.; *Calliderma* Gray; *Iconaster* Slad.; *Gnathaster* Slad.; *Nymphaster* Slad.; *Paragonaster* Slad.; *Mediaster* Slad.; *Nectria* Gray; *Stellaster* Gray; *Ogmaster* v. Martens; *Leptogonaster* Slad.; *Goniodiscus* M. and T.; *Mimaster* Slad.;

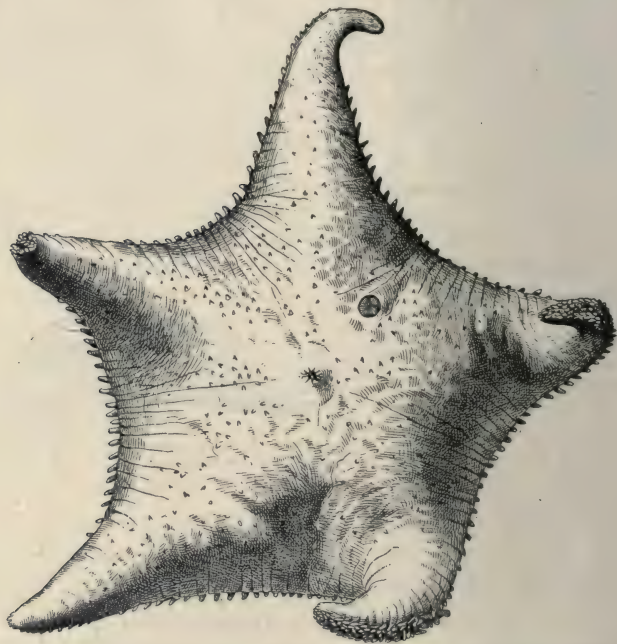


FIG. 138.—*Porania glaber* Sladen, abactinal view (after Sladen).

Anthenoides Perr.; *Hoplaster* Perr.; British species: *Pentagonaster greeni*, Faeroe Channel, 440 fms. *Mimaster tizardi*, Faeroe Channel, 550 fms.

Fam. 5. **Antheneidae.** With well developed marginals, which may bear granules or tubercles. Actinal interradiar areas large and covered with pavement-like plates, which bear large valvate pedicellariae. Anus distinct. *Anthenea* Gray; *Goniaster* L. Ag.; *Hippasteria* Gray.

Fam. 6. **Pentacerotidae.** Dorsal marginals smaller than the ventral, often more or less hidden. Actinal interradiar areas with large pavement-like plates which bear unequal sized granules. With small valvate pedicellariae. Abactinal skeleton reticulate. Anus distinct.

Pentaceros Linck, *Nidorellia* Gray; *Amphiaster* Verrill; *Pentaceropsis*

Slad.; *Culcita* L. Ag.; *Asterodiscus* Gray; *Choriaster* Lütken; *Paulia* Gray.

Fam. 7. **Gymnasteriidae.** Marginal plates large. The whole body is covered with a thick membrane. Arms usually short. Actinal inter-radial areas with large regular plates. Abactinal skeleton tessellate. Anus distinct. *Asteropsis* M. and T.; *Dermasterias* Perr.; *Gymnasterias* Gray; *Tylaster* D. and K.; *Porania* Gray (Fig. 138); *Marginaster* Perr.; *Rhegaster* Slad.; *Poraniomorpha* D. and K.; *Lasiaster* Slad. British species: *Porania pulvillus*. E. N. Atl., to 106 fms.

Fam. 8. **Asterinidae.** With small, sometimes inconspicuous marginal plates. Abactinal skeleton composed of imbricating plates notched on one side and bearing spines on the free margin. Actinal interradial areas with imbricating plates bearing spines. No pedicellariae.

Cyathra J. Bell; *Ganeria* Gray; *Patiria* Gray; *Nepanthia* Gray; *Asterina* Nardo; *Disasterina* Perr.; *Palmipes* Linck; *Stegnaster* Slad; *Tremaster* Verr. British species: *Asterina gibbosa*, E. N. Atl., to 35 fms. *Palmipes placenta*, shores of Britain, etc., to 30 fms.

Sub-Order 2. CRYPTOZONIA.

Marginal plates inconspicuous. The supra- and infra-marginal plates are often separated by intermediate plates. Papulae not confined to the area bounded by the supra-marginals, but found also between the marginals and on the ambulacral surface. Ambulacral plates crowded and narrow. Tube-feet often in four rows. Ambulacrals or adambulacrals of the oral skeleton prominent. Pedicellariae stalked or sessile.

Fam. 1. **Linckiidae.** Marginal plates comparatively well developed, and in contact. Disc small, arms long. Abactinal skeleton tessellate. Pedicellariae (rarely present) excavate or foraminate.

Chaetaster M. and T.; *Fromia* Gray; *Ferdina* Gray; *Ophidiaster* Ag.; *Pharia* Gray; *Leiaster* Peters; *Linckia* Gray; *Phataria* Gray; *Nardoa* Gray; *Narcissia* Gray; *Metrodora* Gray.

Fam. 2. **Zoroasteridae.** Marginal plates in contact. Disc small; arms long, cylindrical, and tapering. Integumentary skeleton spiny. Abactinal skeleton tessellate, arranged in regular longitudinal and transverse series. Primary apical plates persistent and distinct in the adult. Tube-feet conical, terminated by a small sucker; they are arranged in four series at the base of the arm, in two series distally. Pedicellariae (forcipulate) stalked. *Zoroaster* W. Thom., for the most part from great depths; *Cnemidaster* Slad.; *Pholidaster* Slad.; *Mammaster* Perr.; *Caly-caster* Perr.

Fam. 3. **Stichasteridae.** Marginal plates in contact. Disc small; arms long, cylindrical and tapering. Integumentary skeleton for the most part granular. Abactinal skeleton tessellate arranged in longitudinal rows. Primary apical plates less distinct. Tube-feet usually cylindrical and with large terminal sucker, arranged in four rows all along the arms. Pedicellariae forcipiform and forciform.

Coelasterias Stimpson; *Stichaster* M. and T.; *Tarsaster* Slad.; *Neomorphaster* Slad.; *Tonia* Gray; *Nanaster* Perr.; *Granaster* Perr. British species: *Stichaster roseus*, Brit. coast, to 200 fms.

Fam. 4. **Solasteridae.** Abactinal skeleton reticulated, with plates carrying on a projecting tubercle a bundle of divergent spines. Actinal intermediate plates more or less developed. Anus distinct. No pedi-

cellariae. *Crossaster* M. and T.; *Solaster* Forbes; *Rhipidaster* Slad.; *Otenaster* Perr.; *Lophaster* Verrill; *Korethraster* W. Thoms.; *Peribolaster* Slad. British species: *Solaster papposus*, E. N. Atl. to 640 fms., *S. endeca*, ditto to 150 fms.

Fam. 5. **Pterasteridae**. With a reticulated dorsal skeleton bearing paxilliform groups of spines. These spines are united together by a membrane (supradorsal membrane) which forms a continuous canopy over the dorsal surface. The chamber so enclosed is said to be a brood-chamber, and opens to the exterior centrally by a valvular aperture, and by a number of small contractile pores in the supradorsal membrane, and at the side of the arms by apertures regularly recurring over each adambulacral plate and called the segmental apertures. The canopy is present in all specimens hitherto examined; it is uncertain whether these specimens are females or hermaphrodites or whether the canopy is present in both sexes. The supradorsal membrane may in some forms be wholly or partially aborted. Actinolateral spines when present united by membrane so as to form a web on the actinal surface. Pedicellariae absent.

Pteraster M. and T.; *Retaster* Perr.; *Marsipaster* Slad., from the deep sea; *Calyptaster* Slad.; *Hymenaster* W. Thoms., almost entirely an abyssal form; *Benthaster* Slad., from the deep sea; *Myxaster* Perr.; *Cryptaster* Perr. The above are disco-pentagonal in form and have a supradorsal membrane with segmental apertures. *Pythonaster* Slad., stellate forms without supradorsal membrane, actino-lateral spines and segmental apertures, from the deep sea.

Fam. 6. **Echinasteridae**. Dorsal skeleton formed of plates disposed in longitudinal and transverse series, or in an irregular network bearing spines. Spines moderate, pointed, naked or covered by a thin membrane containing calcareous granulations. Arms long. Pedicellariae present only in *Acanthaster* and *Valvaster*.

Acanthaster Gervais, with numerous arms (more than 10) and several (5-16) madreporic plates; *Mithrodia* Gray; *Cribrella* Ag. (*Henricia* Gray); *Perknaster* Slad.; *Echinaster* M. and T. (Fig. 118); *Plectaster* Slad.; *Valvaster* Perr., with wide-meshed arrangement of the calcareous plates and large groups of papulae. British species: *Cribrella sanguinolenta*, E. N. Atl., to 1,350 fms.

Fam. 7. **Heliasteridae**. Arms very numerous (more than 25) and short, disc large. Abactinal skeleton reticulate. Tube-feet in four rows. Double interbranchial septa. *Heliaster* Gray.

Fam. 8. **Pedicellasteridae**. Disc small, not sharply marked off from the arms. Abactinal skeleton of the arms reticulated. Tube-feet in two rows. With numerous, large forcipiform pedicellariae. Genital organs open on the disc. *Pedicellaster* Sars; *Coronaster* Perr., with numerous arms; *Lytaster* Perr.; *Gastraster* Perr.

Fam. 9. **Asteriidae**. With reticulate abactinal skeleton, bearing isolated or grouped spines. Tube-feet in four rows. Pedicellariae forcipiform or forcipiform. Members of this family which have more than five arms are called *heteractinides*: in such species the number may be constantly six, or the number may be subject to individual variation.

Pycnopodia Stimpson; *Coscinasterias* Verrill; *Polyasterias* Perr.; *Stolasterias* Slad.; *Leptasterias* Verrill; *Asterias* L.; *Diplasterias*, Perr.; *Smilasterias* Slad.; *Sporasterias* Perr.; *Anasterias* Perr.; *Hydrasterias* Slad.; *Cosmasterias* Slad.; *Podasterias* Perr.; *Uniophora* Gray; *Calvasterias* Perr. British species: *Asterias glacialis*, E. N. Atl., to 66 fms.,

A. rubens, ditto to 110 fms., *A. muelleri*, ditto, 53 to 433 fms., *A. murrayi*, W. coast Scotland and Ireland.

Fam. 10. **Brisingidae**. Arms long, marked off from the disc (Fig. 139). Marginals absent or vestigial. Abactinal skeleton absent or present only on the ovarian regions. Tube-feet biserial. Genital organs opening on the sides of the arms. Somewhat ophiurid-like in appearance. For the most part in deep water.

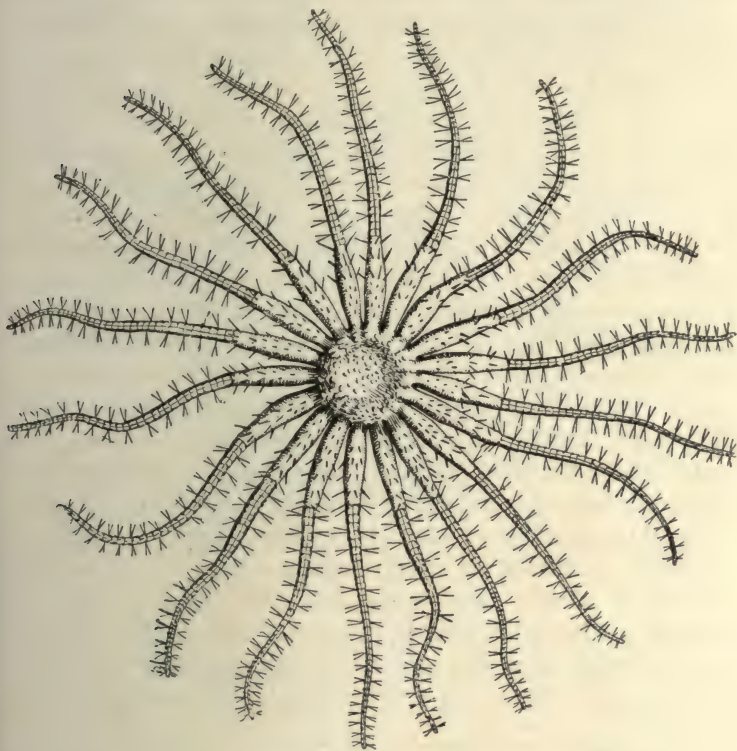


FIG. 139.—*Odinia elegans* E. Per., abactinal view (after E. Perrier).

Hymenodiscus Perr.; *Gymnobrisinga* Studer; *Brisinga* Asbjörnsen; *Odinia* Perr.; *Freyella* Perr.; *Colpaster* Slad.; *Brisingaster* de Loriol; *Labidiaster* Lütken. British species: *Brisinga endecacnemos* and *coronata*, E. N. Atl., 100 to 1,300 fms.

The starfishes of the abyssal regions of the ocean belong to the families *Brisingidae*, *Pedicellasteridae*, *Zoroasteridae*, *Stichasteridae*, *Pterasteridae*, *Pentagonasteridae*, *Archasteridae*, *Porcellanasteridae*. But these are not exclusively abyssal, having littoral representatives in various parts of the world.

Class OPHIUROIDEA *

Brachiate Echinoderms with the body flattened in the or-anal axis. The arms are sharply marked off from the disc and are without an ambulacral groove. The madreporite is on the oral surface.

The Ophiurids are brachiate Echinoderms, and the arms which are very rarely more than five in number (e.g. *Ophioglypha hexactis* with 6 arms, *Ophiocantha vivipara* 6 or 7 arms, *O. anomala* and *nodosa* 6 arms etc.) are sharply marked off from the disc. The ambulacral grooves are absent or so slightly marked as not to be noticeable, and in most forms the ambulacral nerve tracts are separated from the ectoderm by calcareous plates. The generative organs usually open into special pockets developed on the oral side of the disc at the base of the arms and called the genital bursae. The alimentary canal is without an anus and is not prolonged into the arms. The water-pore (or pores) is on the oral surface of the disc, and interradial in position. There is an axial sinus, axial organ, and generative rachis. The tissue of the so-called vascular system is feebly developed, and the tube-feet are without ampullae. As stated above the arms are rarely more than five in number, but in the *Cladophiuræ* they may be much branched (Fig. 146).

The integument is not ciliated, and except in the *Cladophiuræ* and perhaps some *Streptophiuridae* the ectoderm is not present as a layer distinct from the dermis. The dermis is without muscles, but in all Ophiuroids, except the *Cladophiuræ*, is richly provided with calcareous plates. As a general rule these plates form a complete dermal armour which may or may not be

* A. Ljungman, *Ophiuridea viventia huc usque cognita*, Stockholm, 1867. H. Ludwig, *Trichaster elegans*, *Z.f.w.Z.*, 31, 1878. *Id.*, Das Mundskelet der Asterien u. Ophiuren, *Ibid.*, 32, 1879. *Id.*, Zur Ent.d. Ophiurenskeletes, *Ibid.*, 36, 1882. *Id.* Ophiopteron elegans etc., *Ibid.*, 47, 1888. Th. Lyman, Report on the Ophiuridea, *Challenger Reports*, 5, 1882. *Id.*, Ophiuridae and Astrophytidae *Illustrated Catalogue of the Museum of Comp. Anat. of Harvard College*, I. Cambridge, Mass., 1865. L. Cuénot, Etudes anatomiques sur les Ophiures, *Arch. Zool. Exper. et gen* (2), 6, 1888, p. 33. E. W. MacBride, Development of the genital organs, etc., in *Amphiura squamata*, *Q.J.M.S.*, 34, 1893. F. Jeffrey Bell, A Contribution to the Classification of Ophiuroids, etc., *Proc. Zool. Soc.*, 1892, p. 175. J. W. Gregory, Classification of the palaeozoic Echinoderms (Ophiuroidea), *Proc. Zool. Soc.*, 1896, p. 1028. Lütken et Mortensen, The Ophiuridae, *Mem. Mus. Harvard College*, 23, 1899. O. Hamann, Ophiuroidea, in *Bronn's Thierreich*, 1900-1901.

covered by a soft integument, but in the *Cladophiuræ* and some *Streptophiuridae* the skeletal plates of both the disc and the arms are much reduced, and the integument is soft and thick.

The skeleton of the arms consists of a double row of internally-placed ossicles which are generally fused with each other in pairs and are comparable to the ambulacral ossicles of *Asteroids*

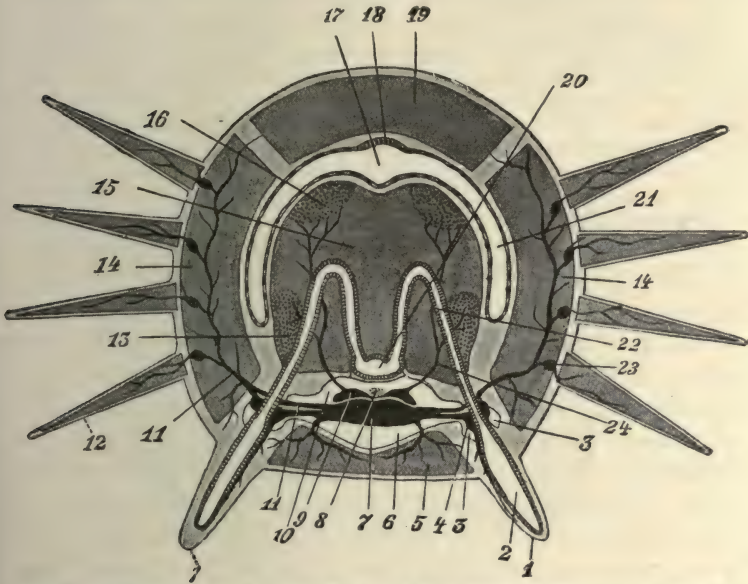


FIG. 140.—Transverse section through the arm of an Ophiurid, diagrammatic (from Lang). 1 tube-foot (ambulacral tentacle); 2 its cavity; 3 epineural circular canal; 4 circular ganglion, both at the base of the tentacle; 5 under arm plate; 6 radial epineural canal; 7 radial nerve trunk of the superficial oral system (ambulacral nerve); 8 radial blood-vessel; 9 radial trunk of the deep oral nervous system (Lange's nerve); 10 radial periahaemal canal; 11 peripheral branch of the radial nerve; 12 spine; 13 lower intervertebral muscle; 14 lateral plate; 15 ambulacral (vertebral) ossicle; 16 upper intervertebral muscle; 17 brachial coelom; 18 specially ciliated strip of peritoneum; 19 upper arm plate; 20 radial water-vascular trunk; 21 lateral portions of the brachial coelom which are repeated in each brachial segment; 22 branch of water-vascular trunk to tube-foot; 23 ganglion at base of spine; 24 motor nerve from deep oral nervous system.

(Fig. 140, 15). The water-vascular trunk, periahaemal canal and nerve cords lie on the lower side of these ossicles and a prolongation of the perivisceral space on the dorsal (17).

The outer or ambital skeleton of the arm is segmented. Each segment consists of four plates; a median under arm-plate, a median upper arm-plate, and two lateral arm-plates (Fig. 140). These plates join one another and the corresponding plates of

the adjacent segments, except in those forms in which the skeletal plates are deficient (Cladophiuræ, some Streptophiuridae) and the arms have a soft integument which contains only small skeletal pieces. The lateral arm-plates, which are generally compared to the adambulacral plates of Asteroids, carry spines, the others do not. The tube-feet emerge through openings between the under and lateral plates, one pair in each arm-segment. At the edges of these apertures are small scales.

The ambulacral or vertebral ossicles arise as separate pieces, which generally fuse together in pairs. In certain deep sea forms (*Ophiohelus*) each of these has the form of a curved rod joined to its fellow at each end. The successive ossicles movably articulate with one another and are attached by muscles (Fig. 140, 13 and 16). The articular surfaces vary in form and may develop processes and pits analogous to the zygosphenes and zygantra of an ophidian vertebra; but sometimes the articulating surfaces are simple and the arms have a greater power of movement (*Astrophyton*, etc.). The radial water-vascular trunk lies in a groove on the lower side of the ambulacral ossicles, and its branches in passing to the tube-feet have a curved course through these structures (Fig. 140).

Spines are present on the lateral plates of the arms, and occasionally on the upper surface of the disc and on the lower surface between the arms. In *Ophiopteron elegans* some of the arm-spines of each arm-joint are united together by a thin transparent membrane, thus forming a series of lateral fins. Pedicellariæ of the ordinary type are not present, but in some forms (Cladophiuræ) movable hooks, generally articulated to a pedicle, are found on certain parts of the arm. The hooks which occur in pairs are not opposed but move parallel to one another. Such modified pedicellariæ are found in *Astrophyton*, *Ophiothrix fragilis*, *Trichaster elegans*. The absence of true pedicellariæ in Ophiurids would appear to militate against the view that pedicellariæ play an indispensable part in keeping the skin of Echinoderms clear of foreign growths and débris.

The lower skeletal pieces of the disc constitute the oral skeleton and are very complicated. They comprise the proximal ambulacral and adambulacral (lateral) brachial plates, and the inter-radial buccal shields, on one or all of which are the water pores (see below), and a number of accessory pieces which belong to the ambital skeleton.

The integument on the lower side of the disc between the insertions of the arms is either soft and contains small isolated skeletal pieces or granules, or is provided with a layer of imbricating plates. The bursal

apertures which in some species are double (*Ophioderma*) are placed on the lower side of the disc, one on either side of the insertion of each arm. The *genital plate* (Fig. 141, *gp*) is a skeletal piece placed on the radial side of each of these slits.

In a view from the inner side (Fig. 141) the angles are seen to consist of four plates; the two oral-angle plates ($am_2 + ad_1$) and the peristomial plates (am_1). The oral-angle plates meet at the torus angularis (*ta*) and diverge outwards and towards the radii. Each of them has on the side towards the buccal fissure two depressions for the oral tube-feet (Fig. 141, *pteb*) and carries on its lower edge a number of small spines; of these some project into the buccal fissures and are called *oral papillae* (Fig. 142, 10),

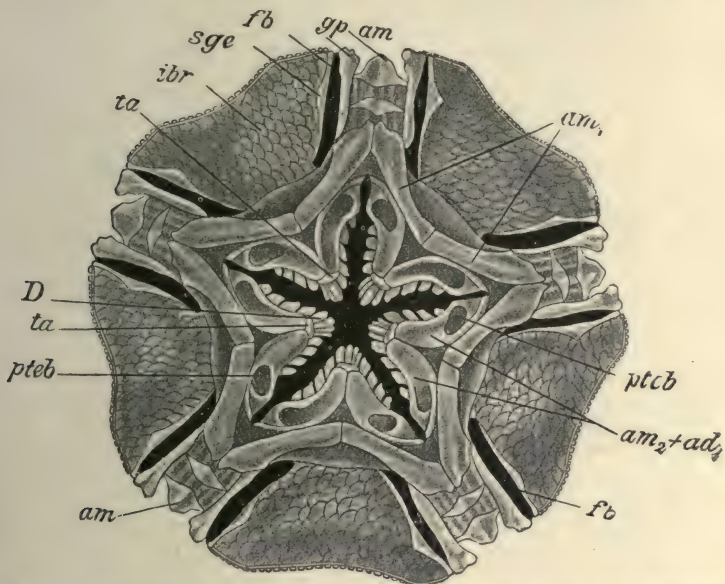


FIG. 141.—Oral skeleton of *Ophiopyren longispinus* Lym., from within (from Lang after Lyman). *am* ambulacral ossicle; *am₁* peristomial plates, supposed to be the ambulacral ossicle of the first brachial segment; $am_2 + ad_1$ oral-angle plates; *D* teeth; *fb* bursal apertures; *gp* genital plate; *ibr* interbrachial region; *pteb* depressions for oral tube-feet; *sge* bursal plate; *ta* torus angularis.

while others arise nearer the angle and project towards the centre of the mouth and are called *dental papillae*. The dental papillae are above the teeth of the torus angularis. The oral-angle plates are supposed to consist of the adambulacral (lateral) plate of the first brachial segment (next the angle) and of the ambulacral ossicle of the second brachial segment (outer part of oral-angle plate).

The peristomial plates (am_1) are on the inner side of the oral-angle plates and are supposed to represent the ambulacral ossicles of the first brachial segment.

At the outer end of each buccal fissure is a plate (Fig. 142, 8) which is supposed to be the under plate of the second brachial segment; dorsally to this there may be sometimes made out another piece which is supposed

to represent the under plate of the first brachial segment. The mouth is a star-shaped aperture with the five interradial angles projecting into it (Fig. 142). These angles are formed externally of four plates: the oral plate or buccal shield (7), of two lateral buccal plates (5) lying on the sides of the buccal shield and meeting on the oral side of it, and of the *torus angularis*, which carries teeth. The lateral buccal shields are supposed to be the modified adambulacrals (laterals) of the second brachial segment. The torus angularis consist of a vertical row of pieces which may fuse together (Fig. 141, *ta*). The slits between the angles are called the buccal fissures.

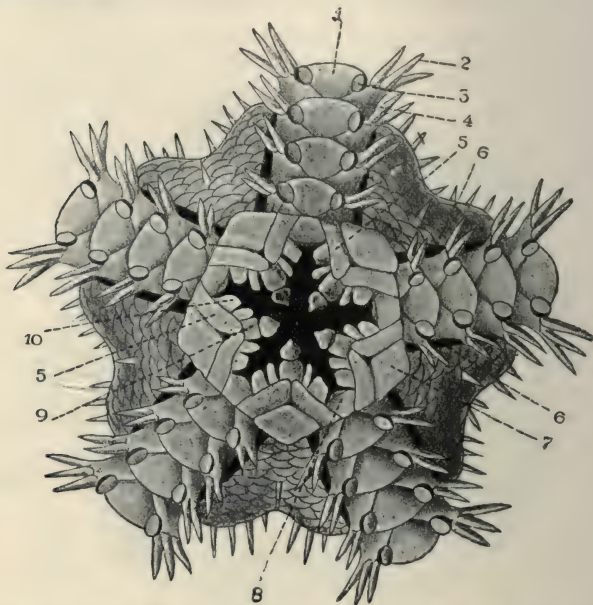


FIG. 142.—Lower surface of disc and base of arms of *Ophiactis poa* Lym. seen from the outside (from Lang after Lyman). 1 under plates; 2 spines of the lateral plates; 3 tentacle scales; 4 lateral buccal shields; 5 apertures of bursae; 6 buccal shields; 7 first under plate of arm (supposed to belong to the 2nd brachial segment); 8 torus angularis; 9 oral papillae.

The skeleton of the disc. The upper skeletal plates of the disc consist principally of the plates of the primary apical system, but there are generally other plates as well, and these may be so numerous as to completely obscure the primary plates. Moreover the completeness of the system of primary apical plates varies even in the same genus. In a typical case the arrangement of plates on the upper side of the disc is as follows (Fig. 143): a central plate surrounded by five radials (*r*) and five basals (*ba*); the radials are separated from the central by the

infrabasals, beyond this system are the ten radial shields (*rs*) and the five second interradials (*ir*), which do not belong to the primary apical system.

The completeness of the apical system varies much in the group. In some forms, the embryonic condition is retained, but even here it may be reduced to the central and five radials, or central and five basals. Not infrequently it happens that the integument of the disc is soft and the plates small, scattered and inconspicuous. The radial shields are perhaps the most constant and conspicuous of the upper skeletal plates of the disc (including the apical system). They sometimes reach from the base of the arm to near the centre of the disc.

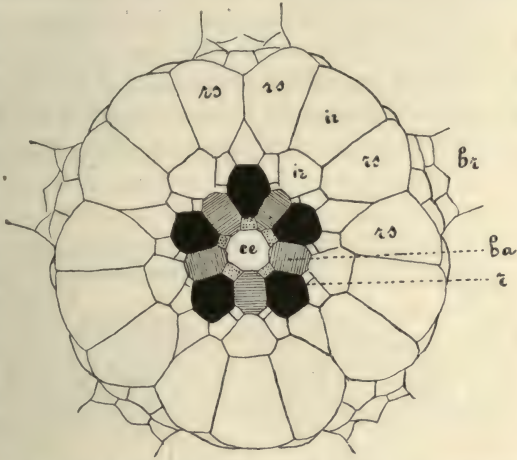


FIG. 143.—Plates of the upper surface of the disc of *Ophiomusium validum* (from Lang, after P. H. Carpenter). *ce* central plate; *r* radial, *ba* basal plates; the dotted plates between the basals and the central are the infrabasals; *ir* interradial plates; *rs* radial shields; *br* arms.

At the end of each arm there is a median termi-

nal plate which differs from the terminal plate of Asteroids in the fact that it not only lies over the terminal unpaired tentacle of the water-vascular system, but completely surrounds it.

The **alimentary canal**, the mouth of which has already been described, leads by a short oesophagus into a large stomach (Fig. 144). The stomach is without any special glandular appendages and there is no anus.

The **nervous system** is arranged very much as in Asteroids, except that the ectoneural plexus is absent in those forms in which the epithelium of the ectoderm is reduced, and that the ventral system (circumoral ring and ambulacral nerves) is removed from the surface and lies in the wall of an epineural canal (Fig. 140, 7). This canal, which is lined by ectoderm, being developed as an ectodermal groove, is covered ventrally by calcareous plates. It is found in connexion with the circumoral

ring as well as with the radial cords. The latter are swollen into ganglia at the points where the nerves come off.

The deeper oral system consists of two trunks in each arm placed close together and just above the radial trunks of the superficial system (Fig. 140, 9). They innervate the inter-vertebral muscles (Fig. 140) and are continued into a circum-oral band in the disc. The apical nervous system appears not to be represented, unless the genital nerve ring which runs in the wall of the aboral sinus belongs to it. The tube-feet are all sensory structures, and are supplied by a branch from the ambulacral nerve (Fig. 140, 4), which dilates into a ganglion at

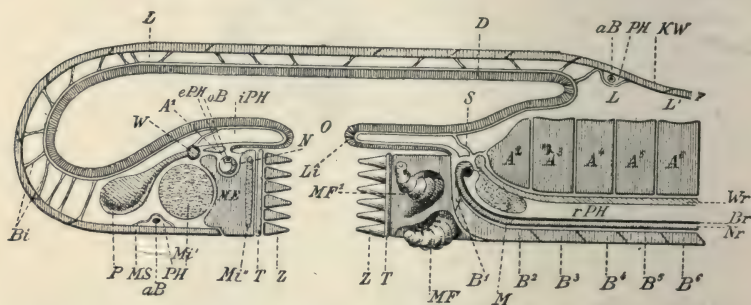


FIG. 144.—Diagrammatic vertical section through the disc and one radius of an Ophiurid (*Ophioglypha*), from Perrier, after Ludwig. A^1 peristomial plate (1st ambulacral); A^2 – A^6 2nd to 6th ambulacral plates; aB generative rachis; B^1 – B^6 the 1st to the 6th ventral plates (under arm plates); Bi mesenterial filaments attaching the stomach to the body-wall; Br radial blood-vessel; D stomach; ePH circumoral periaermal sinus; iPH periesophageal part of perivisceral cavity; KW body wall; L body-cavity of disc; L^1 of arm; Li lip; M , Mi^1 , Mi^{11} muscles of the oral skeleton; ME oral angle plate; MF and MF^1 first and second oral feet; MS buccal shield; N nerve ring; Nr radial nerve; O mouth; oB circular blood-vessel; P polian vesicle; PH aboral sinus; rPH radial periaermal canal; S septum which separates the periesophageal sinus from the rest of the perivisceral cavity; T torus angularis; W water-vascular ring; Wr radial water vessel; Z teeth.

their base. There is no eye, but the ambulacral nerve trunk becomes epithelial in position on the terminal tentacle.

The general arrangement and relations of the **coelom** are the same as in Asteroids, the principal difference consisting in the ventral position of the madreporite.

The general body-cavity or **perivisceral cavity** is in relation with the stomach in the disc and is prolonged into the arms on the dorsal side of the ambulacral ossicles (Fig. 140). The portion in the disc is traversed by connective tissue strands (Fig. 144), and is divided into two parts by a septum connecting the oesophagus with the oral skeleton (S). A small periesophageal

sinus (*iPH*) is thus cut off from the main portion. The brachial portion is dilated segmentally over each pair of ambulacral ossicles. The walls between these dilatations or chambers are imperfect and are traversed by calcareous plates which connect the ambulacral ossicles with the plates of the ambital skeleton. There is a streak of epithelium carrying specially strong cilia in the upper wall of the brachial continuation of the perivisceral coelom (Fig. 140, 18).

The **water-vascular system** is almost exactly as in Asteroids. It consists of a circumoral vessel sending off a prolongation along each arm. This gives off lateral branches to the tube-feet which however are *without ampullae* and are purely sensory in function ; it ends in the terminal tentacle. The first two pairs of tube-feet are in relation with the mouth as *oral tentacles* (see p. 197), and are supplied by canals which arise from the circumoral vessel. There is a **polian vesicle** in each interradius except that of the stone-canal. In *Ophiactis virens*, which has several stone-canals, there are not only two or three polian vesicles in each interradius, but also a number of tubular prolongations (canals of Simroth) of the circumoral vessel which encircle the intestine and penetrate between the generative organs. These tubes are supposed to be respiratory in function, a view which is suggested by the fact that the genital bursae are absent in this species.

The stone-canal (Fig. 145, 2), which however is without any calcareous matter in its walls, passes ventralwards to open into the ampulla (3), which corresponds to the whole of the axial sinus of Asteroids and opens to the exterior by the pore-canal (4) on the ventral surface of the disc, on one of the buccal shields (oral plates). The opening of the water-pore is placed asymmetrically on the oral plate on an edge of it adjacent to a bursal slit. As a rule there is only one water-pore, but in some species of many genera of *Ophiuræ* (*Amphiura*, *Ophiolepis*, *Ophiopocus*, *Ophionereis*, *Ophiocnida*), and in all *Astrophytidae* there are several pores on the buccal shield concerned. In *Trichaster elegans*, there are five stone-canals and five water-pores, one in each interradius. In *Ophiactis virens*, which reproduces itself by division, the stone-canals are repeated in several interradii. In these cases of repetition of the stone-canals, the young forms are said to have only one.

Some or all of the corpuscles in the water-vascular fluid of *Ophiactis virens* are coloured red with haemoglobin.

The **axial organ** has the same structure as in Asteroids. It is found on the side of the stone-canal turned away from the mouth (Fig. 145). It is in relation with a section of the body cavity (Fig. 145, 7), which is quite unconnected * with the ampulla (axial sinus) and is probably the diverticulum of the left posterior body-cavity of the larva which is formed in the invagination of the primitive germ-cells (MacBride).

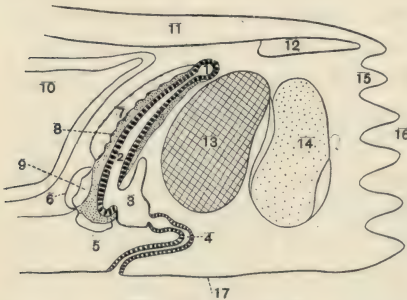


FIG. 145.—Diagram of a vertical section through the madreporitic interradius of *Amphiuura squamata*, showing the relations of the axial organ, stone-canal and neighbouring sinuses (after MacBride). 1 circumoral water-vascular vessel; 2 stone-canal; 3 ampulla (axial sinus); 4 pore-canal; 5 closed sac which appears to represent the right hydrocoel; 6 aboral sinus in its ventral position; 7 sinus derived from the left posterior coelom and sometimes called the axial sinus; 8 axial organ; 9 genital rachis; 10 genital bursa; 11 wall of stomach; 12 peroesophageal sinus; 13 interradial muscle; 14 nerve ring; 15 teeth; 16 mouth; 17 oral surface of disc.

The axial organ (Fig. 145, 8) is continuous with the generative rachis, which is contained in the aboral sinus (Fig. 144, PH) (a portion of the left larval coelom as in Asterids) and takes a somewhat peculiar course round the disc. Radially it lies in the aboral part of the disc between the stomach caecum and the upper integument, whereas in each interradius it dips down between the stomach caeca towards the lower surface (Fig. 144). It has been suggested that this course

is due to the fact that, in the interradii, structures which were originally on the upper side of the disc have moved on to the lower surface; as an instance of this may be cited the water-pore which in the young form is dorsal, but in all adults has passed on to the ventral surface.

The perihaemal system consists of a circumoral canal which is prolonged into a radial tube in each arm on the upper side of the nerve cords (Figs. 144, *ePH*; 140, 10). There does

* Cuénot, who thought that the two are in communication, appears to have been in error. His mistake is reproduced, together with an erroneous figure, on p. 820 of the section on Echinoderms in Bronn's *Thierreich* (1900).

not seem to be any representative of the inner oral perihæmal ring of Asteroids.

The **vascular tissue** seems to be arranged very much as in Asteroids. In some forms the radial vessels are said not to be present.

The **generative organs**. Most Ophiurids are dioecious, but *Amphiura squamata* is hermaphrodite. The generative glands are simple sacs which open, in all except *Ophiopus* and *Ophiactis virens*, into the genital bursæ.

The genital **bursæ** are five pairs of sac-like invaginations of the interradial portions of the lower wall of the disc, and project into the body-cavity between the bulgings of the stomach. They open by slit-like apertures (double in *Ophiura*) placed one on either side of the insertions of the arms into the disc (Fig. 142). They have thin walls, lined by a ciliated epithelium and often containing calcareous matter. The **gonads** are small sacs placed on the walls of the bursæ and opening into them. Each generative sac is connected with a branch from the generative rachis, the course of which has been described. The aboral sinus is continued with the rachis to each gonadial sac and invests it as in Asteroids. The generative cells pass into the bursæ and outwards by their slit-like apertures. In many Ophiurids (*Amphiura squamata* and *magellanica*, *Ophiacantha vivipara* and *marsupialis*; *Ophiomyxa vivipara*, etc.) the bursæ act as brood pouches and the eggs develop in them; but the principal function of the bursæ seems to be respiratory, water being continually drawn in and ejected by the ciliary currents, and in some cases by the muscular elevations and depressions of the dorsal surface. In *Ophiactis virens* the bursæ are absent * and the gonads open directly on the lower surface of the disc. They are replaced by the canals of Simroth, which have been already described (p. 201).

The power of regenerating lost parts, e.g. arms, even a portion of the disc, is considerable, but apparently the disc cannot be regenerated from a single arm as in Asteroids. The brittle stars readily lose their arms, so that the power of regeneration is very important.

Reproduction by fission through the centre of the disc has been observed in a few genera (e.g. *Ophiactis*).

* Cuénot, *Arch. Biologie*, 11, 1891, p. 303.

Among preserved Ophiurids many specimens are found in which the dorsal surface of the disc is absent.* The significance of this fact is not understood.

The larval form is the Ophiopluteus† (p. 140). In those forms in which care of the brood occurs there is no free larva. The ophiopluteus may present modifications in which the arms are reduced. Such are *Ophiopluteus metschnikoffi* and *claparedei*. The larvae known as *Ophiopluteus annulatus*,‡ *O. krohnii*, *O. oblongus* are vermiform, without ciliated band and without or with only one skeletal rod. These larvae are pelagic. Including the vermiform larvae about seventeen ophioplutei are known, most of which are as yet unrelated to any adult.

The Ophiuroidea live upon the bottom of the sea and feed upon the minute organisms and organic matter contained in the surface mud, which they take up by means of the buccal tube-feet. They move § fairly actively by means of the lateral flexion of their arms. In some forms the arms possess a power of vertical movement as well, especially towards the end. When the arms are very long they can be moved in a serpentine manner.

The group first makes its appearance in the Upper Cambrian (Ordovician). Its affinities are with the Asteroids, with which it is sometimes united under the superclass Stelleroidea. It is indeed difficult to separate them, especially when the palaeozoic genera (*Eophiura*, *Bohemura*, etc.), recently described by Jaekel, || and such a form as *Astrophphiura* are considered. The principal points of difference relate to the closing over of the ambulacral groove (a feature which is but slightly marked in

* Jeffrey Bell, in Gardiner's *Maldivé and Laccadive Expedition*, 1903, p. 223. Prof. MacBride states that he has seen an *Amphiura squamata* throw off the whole dorsal surface of the disc with the stomach.

† Mortensen, *op. cit.*

‡ This is J. Müller's vermiform asteroid larva, with segmented body (Ueb. d. Larven u. d. Metamorphose d. Echinodermen, Abh. 3, p. 26, Abh. d. Pr. Akad. d. Wiss. zu Berlin, Abh. i.-vii., 1846, 1848-53), and apparently the larva described by Grave (*Mem. Johns Hopkins*, 1900). The latter is at first uniformly covered with cilia, which later become restricted to four bands. These give it a resemblance to an *Antedon* larva, a resemblance which is heightened by the fact that the last trace of the larval organ (preoral lobe) is found at the edge of the aboral surface of the disc. The author does not state whether this organ is encircled by the water-vascular ring as it is in Asteroids.

§ Preyer, *Naples Mittheilungen*, 7, 1886, p. 27.

|| Asteriden und Ophiuriden aus dem Silur Böhmens, *Zeitschr. der deutschen geol. Ges.*, 55, 1903, p. 106. See also Bather's description of a Devonian genus, *Sympterura* (*Geol. Mag.*, 1905, p. 161.)

the *Lysophiuræ* and *Ophioterresis*), the sharp differentiation of the arms from the disc, the absence from the arms of any prolongation of the alimentary system, and the ventral position of the madreporite. Lastly the free larva has the pluteus form. The closure of the ambulacral groove and the presence of an epineural canal is a feature of some importance and one which the class has in common with Echinoids and Holothurians.

The Ophiuroidea are divided into four orders : (1) the *Lysophiuræ*, which are palaeozoic forms in which the ambulacral ossicles alternate ; (2) the *Zygophiuræ* (brittle-stars) in which the system of dermal plates is well developed and in which the arms cannot be rolled up ; (3) the *Streptophiuræ*, which are also brittle-stars, but which approach in some of their characters the *Cladophiuræ* ; (4) the *Cladophiuræ* (gorgon-heads) which have a thick integument with granular deposits without regular dermal plates.

Order 1. LYSOPHIURÆ.

The ambulacral ossicles are alternate and are not united into pairs, but those of each segment are separate. There are no ventral arm plates. All extinct, Silurian and Devonian. *Eophiura*, *Bohemura*, *Symptetura*, *Protaster*, *Bundenbachia*, *Sturtzura*, *Eugaster*, *Ptilonaster*, *Taeniura*, *Palæophiura*.

Order 2. ZYGOPHIURÆ (OPHIURÆ). Brittle-Stars.

The surfaces by which the ambulacral ossicles of the arms articulate with one another are provided with processes and pits which fit into one another and limit the movement of the ossicles upon one another. Upper, under and lateral arm plates are present, and the arms are incapable of coiling round straight rods. The lateral arm-plates bear spines.

1. With arm-spines short, parallel to the long axis of the arms.

Fam. 1. **Ophiodermatidae**. With numerous oral papillae, without dental papillae, with arm incisions on the disc. *Ophioderma* M. and T., *Ophioncus* Ives, *Ophiogona* Stud., *Pectinura* Forbes, *Ophiopezella* Ljg., *Ophiopinax* Bell, *Ophiopeza* Ptrs., *Ophiopyren* Lym. (Fig. 141), *Ophioconis* Ltk.

Fam. 2. **Ophiolepidae**. With 3-6 oral papillae of which the innermost is rarely infradental, without dental papillae, with arm incisions on the disc. *Ophiotrochus* Lym.; *Ophiopaepale* Ljg.; *Ophioceramis* Lym.; *Ophiothyreus* Ljg.; *Ophiolepis* M. and T.; *Ophioplocus* Lym.; *Ophiozona* Lym.; *Ophioplinthus* Lym.; *Ophiolipus* Lym.; *Ophiernus* Lym.; *Ophiophyllum* Lym.; *Ophiochaeta* Ltk.; *Ophiopleura* Dan.; *Ophiopyrgus* Lym.; *Ophiomastus* Lym.; *Ophiomusium* Lym. (Fig. 143), no tentacle pores beyond the basal arm-joints; *Ophiotypa* Khlr.; *Ophiura* Lm.;

Ophiocten Ltk.; *Gymnophiura* Mrtsn. British species: *Ophiura ciliaris*, E. N. Atl., 7-100 fms.; *O. albida*, ditto, to 250 fms., *O. affinis*, ditto, 10-192 fms.

2. Spines at right angles to the arm axis.

Fam. 3. **Amphiuridae**. With 1 to 5 oral papillae, the innermost often infradental. Arms inserted on the ventral side of the disc. Dental papillae absent. *Ophiambyx* Lym.; *Ophiopholis* M. and T.; *Ophiostigma* Ltk.; *Ophiochiton*, *Hemipholis*, *Amphilepis*, *Ophiocnida*, *Ophiophragmus*, *Ophioplax*, *Ophiocytra*, *Ophiomyces*, all Lym.; *Ophiopus* Ljg.; *Ophiactis* (Fig. 142) and *Ophionereis* Ltk.; *Amphiura* and *Ophiopsila* Forbes; *Paramphiura* Khlr.; British species: *Amphiura chiajii*, to 120 fms.; *A. filiformis*, to 120 fms.; *A. elegans*, to 120 fms. *Ophiactis abyssicola*, 64 to 767 fms.; *O. balli*, to 203 fms. *Ophiopholis aculeata* to 300 fms. *Ophiacantha bidentata*, 20-2,335 fms.

Fam. 4. **Ophiophilidae**. Disc with scales and sharp or blunt spines, with teeth and oral papillae, without dental papillae. *Ophiomitra*, *Ophiothamnus*, *Ophiocamax*, *Ophiotholia*, all Lym.

Fam. 5. **Ophiacanthidae**. Disc covered by soft skin, which more or less hides the subjacent scales; dental papillae absent or few. *Ophiacantha* M. and T.; *O. vivipara* Ljn., 6 or 7 arms; *O. anomala* G. O. Sars, 6 arms. *Ophioblebes*, *Ophiotoma*, *Ophiogeron*, *Ophioscisma*, Lym.; *Ophioblenna*, *Ophionema*, *Ophioneptus* Ltk.; *Ophiocentrus* Ljg.; *Ophioscolex* M. and T.; *Ophiotrema* Khlr. Brit. sp.: *Ophioscolex glacialis*, 100-300 fms., *O. purpurea*, 64 to 76 fms.

Fam. 6. **Ophiocomidae**. With oral and dental papillae. *Ophiocymbium* Lym.; *Ophiocoma* L. Ag.; *Ophiarachna* and *Ophiomastix* M. and T.; *Ophiopteris* E. Sm.; *Ophiarthrum* Ptrs. British species: *Ophiocoma nigra*, to 87 fms.

Fam. 7. **Ophiotrichidae**. With 8-10 dental papillae, without oral papillae. *Ophiopteron* and *Ophiotrichoides* Ludw.; *Ophiotrix* and *Ophiocnemis* M. and T.; *Ophiocampsis* Dunc.; *Ophiomaza* and *Ophiopsammium* Lym.; *Ophiothela* Verr.; *Ophiogymna* Ljg.; *Luethenia*, *Gymnolophus*, *Ophioaethiops*, *Ophiosphaera* Brock. Brit. sp.: *Ophiotrix fragilis*, to 52 fms.

Order 3. STREPTOPHIURAE. Astrophyton-like Ophiuræ.

The ambulacral ossicles articulate with one another by means of a more or less simple ball-and-socket joint, and the arms can be moved in a vertical direction and be coiled towards the mouth. Upper, under, and side plates are more or less regularly developed; the side plates bearing spines.

Fam. 1. **Ophiomyxidae**. With 3-7 oral papillae, without teeth. Arms covered with soft skin. *Neoplax* Bell; *Ophioteris* Bell, no under arm-plates; *Ophiobyrsa*, *Ophiochondrus*, *Sigsbeia* and *Ophiobranchion* Lym.; *Ophiomyxa* M. and T.; *Hemieuryale* Martens; *Astrophis* A. M. Edw.; *Ophiohelus*.

Several extinct families come here, viz., **Ophiurinae**, **Lapworthidae**, **Eoluididae**, **Onychasteridae**, **Eucladiidae**. The Eucladiidae from the middle Silurian of England have short arms, and a ventral madreporite. Each arm has 2 or 3 arm-like branches; these are tube-feet with a flexible armour of minute spiny scales. *Eucladia* H. Woodward, *Euthemon* Sollas.

Order 4. CLADOPHIURAE (EURYALAE).

Gorgon-heads.

The ambulacral ossicles articulate with one another by means of hour glass-shaped surfaces and are covered by granular deposits in the thick integument. The arms may be simple or branched repeatedly. They can be moved in the vertical plane and coiled towards the mouth. There are no spines on the sides of the arms. Most of those with unbranched arms have a mouth-shield at the inner angle of each lower interbrachial space, one of which serves as the madreporite. Those with branched arms have often no mouth-shields, and the madreporites, sometimes single, sometimes five in number, are found in various regions of the lower interbrachial spaces. Pedicellaria-like processes are sometimes present.

Fam. 1. **Astrophytidae**. With simple arms. *Astrotoma* Lym.*; *Astronyx* M. and T.*; *Astrochele* Vll.*; *Astrogomphus* Lym.†; *Astroporpa* Örst. and Ltk.†; *Ophiocreas* Lym.‡; *Astrochema* Oerst. and Ltk.‡; *Astrocera* Lym.‡. Brit. sp.: *Astronyx loveni* to 350 fms.



FIG. 146.—*Trichaster elegans* (after Ludwig).

Fam. 2. **Trichasteridae**. The arms branch a few times near their free ends. *Trichaster* L. Ag. (Fig. 146); *Astroclon* Lym.; *Astrocnida* Lym.

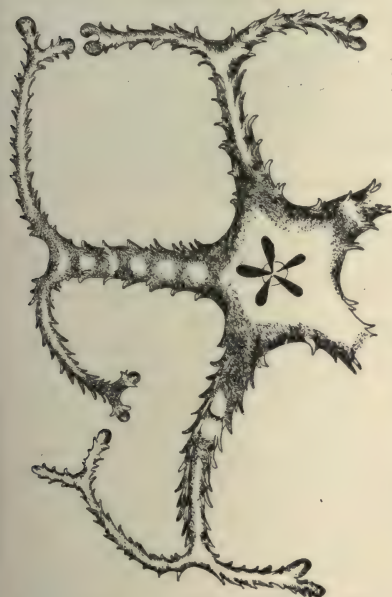


FIG. 147.—Young *Gorgonocephalus agassizi*, ventral view (after Lyman).

Fam. 3. **Euryalidae**. The arms branch much and from near their base. *Euryale* Lmk.; *Gorgonocephalus* Leach (Fig. 147); *Astrophyton* Linck. Brit. sp.: *Gorgonocephalus lincki* and *eucnemis*.

The genus *Astrophysura* Sladen though undoubtedly an Ophiuran presents some Asteroid features. The family **Astrophysuridae** has been created for its reception. The disc is pentagonal and the greater part of the arms are included in it. The free portion of the arms is short, reduced and without tube-feet. There are no teeth and the buccal armature is simple and imperfect. Under arm-plates are present and the cavities for the retracted feet are spacious. The madreporite appears to be ventral. Madagascar and the neighbouring islands.

* Disc large.

† Disc moderate (about one-tenth of length of arms).

‡ Disc small.

Class ECHINOIDEA *

Spherical, oval, or discoidal Echinoderms with a shell composed of calcareous plates usually closely fitting and carrying movable spines. The mouth is on the under surface, and the anus either within the apical system or between the apical system and the mouth. The five ambulacra are indicated by rows of pores and usually extend almost to the aboral pole. There are typically five inter-radial gonads.

The body of an Echinoid is typically spherical, but is often heart-shaped, oval, or flattened. There are no arm-like prolongations, but there is a five-rayed symmetry in the build of the body as is shown by the disposition of the water-vascular, nervous and other systems of organs. The dermal skeletal plates, which are pentagonal or hexagonal in shape, are connected together so as to form, with rare exceptions (Echinothuridae, which see, and certain Palaeoechinoidea, plates of posterior ambulacrum of some Spatangids, peristomial plates of Cidaroida), a firm immovable skeleton, the test or shell. The mouth is on the lower surface of the body, generally in the centre, but sometimes shifted towards what is called the anterior end; the apical system is on the upper surface and the anus is either within it (*Endocyclica*) or outside it (*Exocyclica*).

* A. Agassiz, *Revision of the Echini*, Cambridge U.S.A., 1872-4. Id. Report on the Echinoidea, *Challenger Reports*, 1881. Id. Panamic deep-sea Echini, *Mem. Mus. Harvard College*, 31, 1904. Cotteau, Echinides, *Paléontologie Française*, 7, 9, 10, Paris 1862-79. P. Martin Duncan, A revision of the genera and groups of the Echinoidea. *Journ. Linnean Society*, 23, 1891. S. Lovén, Études sur les Echinoides, *Kongl. Svenska Vetenskaps-Akademiens Handlingar*, 11, 1872; a translation in *Ann. and Mag. Nat. History* (4), 10, 1872. C. F. and P. B. Sarasin, *Üb. d. Anat. d. Echinothuriiden etc. Ergebnisse Nat. Forschungen Ceylon*, 1, 1888. Id., Die Auge etc. der Diadematiden, *ibid.* 1, 1887. J. Müller, L. Cuénot, O. Hamann, *Delage Op. cit.* Prouho, Recherches sur le Dorocidaris papillata, etc., *Arch. Zool. Exp. et gen.* (2), 5, 1888, p. 213. O. Hamann, Echinoidea in Bronn's *Thierreich*, 1901-1905. Th. Mortensen, Echinoidea (Pt. 1), in the *Danish Ingolf-Expedition*, I, vol. 4, 1903. F. Leipoldt, Das angebliche Excretions-organ der Seeigel, *Z.f.w.Z.*, 55, 1893, p. 585. S. Lovén, on Pourtalesia, *K. Svenska Vet. Akad. Handl.* 19, 1884. Id., Echinologica, *Bih. Svenska Vet. Akad. Förhdt.*, 13, 1887. Id., Echinologica, *Bih. Svenska Vet. Akad. Handl.*, 18, 1892. H. Theél, On the development of *Echinocyamus pusillus*, *Nova Acta R. Soc. Sci. Upsala*, 1892. Id., Prel. acc. of the devel. of *Echinus miliaris*, *Bih. Svenska Akad. Handl.*, 28, 1902. E. W. MacBride, Dev. of *Echinus esculentus* etc., *Phil. Trans.*, 1903, p. 285.

When the anus is outside the apical system, it always lies in what is called the posterior interradius (V. I). The outline of an Echinoid shell when viewed from the apical pole is called the **ambitus**. The plates of the skeleton are covered by the ciliated epidermis and lie entirely superficial to the nervous and water-vascular systems; they are perforated by apertures for the passage of the tube-feet, and bear prominences and tubercles to which the variously shaped spines are movably articulated. The apical system is very limited in extent and takes up the whole of the abambulacral surface of the body (Fig. 149). The

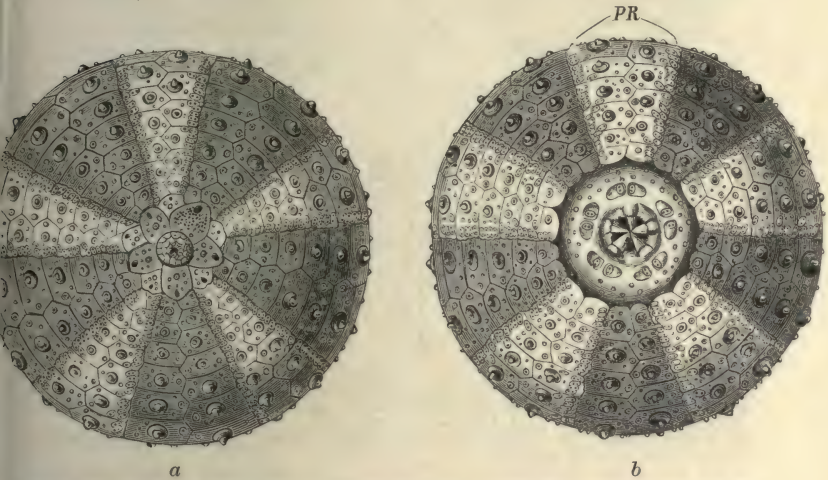


FIG. 148.—Test of a young regular sea-urchin *Strongylocentrotus droebachiensis* (from Claus). *a* from the aboral side; *b* from the oral side. *PR* rows of pores in the anterior radius. The peristomial membrane contains the mouth with 5 teeth in the centre and 5 pairs of plates perforated by pores for the oral tube-feet.

madreporite is on the upper surface and is one of the apical plates, generally the basal of what is called the right anterior interradius (II, III). For purposes of description, there may be said to be two principal kinds of Echinoids, the regular forms, in which the body is more or less spherical and the anus is within the apical system (Endocyclica, Regularia), and the irregular forms, in which the body is oval, or heart-shaped, and more or less flattened in the principal axis, and in which the anus is outside the apical system in the posterior interambulacrum (Ectocyclica, Irregularia). The test consists of the plates of (1) the apical system, and (2) the **corona** or rest of the shell;

to these may be added the peristomial plates, i.e. the plates in the peristomial membrane in the middle of which the mouth is placed (Fig. 148 b).

In the regular forms or **Endoecyelica** (Diadematoidea, Cidaroida, most Palaeoechinoidea), the **apical system** (Fig. 149) consists of (1) the periproct area containing a number of small plates, the *periproct plates*, amongst which, towards the right posterior



FIG. 149.—Apical plates of young *Strongylocentrotus droebachiensis* (from Lang, after Lovén). *an* anus among the periproct plates; *go* genital openings on the basal or genital plates; *m* madreporite (right anterior basal); *r* radial plates (ocular).

radius (No. I) or interradius (I. II) lies the *anus* (*an*); (2) the five interradially placed *basals* (*genitals*), which are usually perforated each by a genital opening (*go*), and one of which (*m*) is perforated by the water-pores of the madreporite. With this system, though not belonging to it, must be mentioned the five radially placed ocular plates (*radials*) which are perforated for the small terminal

tentacles of the water-vascular system: these plates are really the terminals and belong to the ambulacral surface. Some or all of the radials may be wedged in between the basals and assist in forming the boundary of the periproct.

Occasionally, as a specific or individual character, more than one genital opening is present on each genital plate. Thus two pores have been found in *Cidaris perornata*, *Arbacia punctulata*, etc., five on the madreporite of *Echinus acutus*. In short, among both fossil and recent species there is some variability in this character.*

In the young of the *Saleniidae* the centre of the apical system is occupied by a *central*, on one side of which, in the right posterior interradius, the anus is placed. This condition is repeated in most young sea-urchins (Fig. 150), but in adults a number of small plates—the periproct or

* In the cretaceous and tertiary genus *Goniopygus* (Arbaciidae) the genital openings are outside the apical system.

anal plates are added and the central becomes indistinguishable. The anus is always excentric, being displaced towards the right posterior interradius (as in Asterids).

The *test* or *corona* consists of ten double meridional rows of plates passing round from the apical to the oral pole (Fig. 148). Five of these double rows are radial in position and constitute the *ambulacra*, while five are interradial and are called the *interambulacral* plates.

This statement is true of all *Euechinoidea*.* In the *Palaeoechoinoidea*, however, the number of rows of plates in the interambulacra is either one (*Bothriocidaris*) or more than two (from 3 to 11).

The plates are pentagonal in form and are so placed that the median suture between the two rows of an ambulacrum is zigzag (Fig. 148), while the suture separating an ambulacrum from an interambulacrum is straight. Each plate of an ambulacrum is perforated by two pores, called *double pores* or *pore-pairs*; these are placed on the side next the adjacent interambulacrum and give exit to the two tubes which pass from each ampulla inside to each projecting tube-foot outside (Fig. 169). When there are more than one double pore upon an ambulacral plate, as often happens, the plate is composite and consists of as many plates, fused together, as there are double pores upon it (Fig. 151).

When the ambulacral plates are compound, the word **primary** † is applied to a component which reaches right across from the ambulacro-interambulacral suture (outer suture) to the median suture between the two rows of ambulacral plates; **occluded** to a plate which reaches the median, but not the outer suture; **isolated** to a component cut off from both sutures; **demiplate** to a component which reaches the outer, but not the median suture.

The growth of the shell is effected partly by increase in size of the plates already present and partly by the addition of new plates just out-

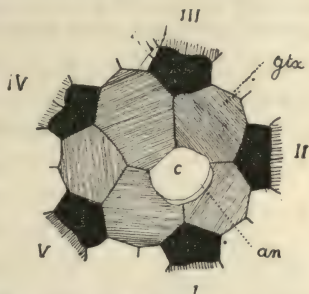


Fig. 150.—Apical system of a young *Echinus* (from Delage, after Lovén). An anus; *c* central; *gla* one of the genital plates. I. to V. indicates the enumeration of the radii adopted in this work. The anus is shifted towards interradius No. I. II., and the madreporite is on the basal of interradius No. II. III.

* Except the cretaceous genus *Tetracidaris*, in which there are four rows of interambulacral plates.

† The word *primary* is sometimes used for the component elements of a composite plate.

side the apical system. The ambulacral plates so formed are biporous and of similar size and shape. In many forms they retain these characters, and the ambulacral plates are simple and biporous. In other cases they soon become unequal in size and fused together to form compound plates, in which there are two, three or more pairs of pores. The growth of the ambulacra and interambulacra are quite independent of one another. According to Lovén the peristomial plates of the *Cidaridae* are detached successively from the corona and are formed in the same manner, but earlier, as are the other plates of the corona.

The plates of the ambulacrum next the peristome are called the *marginal ambulacral* plates. Apically an ambulacrum ends in one of the ocular (radial) plates.

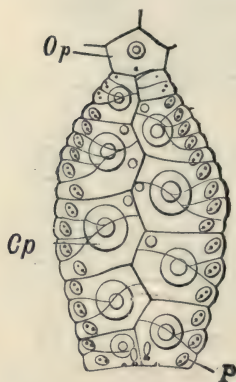


FIG. 151.—Third ambulacrum of a young *Strongylocentrotus droebachiensis* of 3 mm. (from Claus, after Lovén). *Op* radial plate; *P* primary plate and double pore; *Cp* tubercle for spine. The ambulacral plates are compound and the sutures are visible.

In the interambulacra the plates are not perforate nor composite. Apically an interambulacrum abuts upon a genital (basal) plate, and the plates next the peristome are called the *marginal interambulacral* plates. The peristomial margin is often incised, *i.e.* there is a notch between the two peristomial plates of each interambulacrum; these notches are for the passage of the external gills (see p. 231).

The peristomial membrane always contains a number of calcareous bodies, but these in the Spatangoids and Clypeastroids are not perforated and have nothing to do with the ambulacral and interambulacral series of plates. In the Cidaroida, however, both the ambulacral and interambulacral plates are continued on to the peristome, and are flexibly joined together by mem-

brane. In the Diadematoidea it contains (except in the Echinothuridae, in which the ambulacral series of plates is continued up to the mouth) five pairs of perforated ambulacral plates (Fig. 148), which carry the buccal tentacles (see p. 233).

In the irregular forms or **Exocyclica** (Holoctypoida, Clypeastroida, Spatangoida) the anus and periproct are not contained within the apical system which keeps its position at the upper pole, but lie at some point in the posterior interradius, either on the upper surface of the shell or at the ambitus or on the lower surface (Figs. 152, 153). The Holoctypoida alone retain the spherical and radiately symmetrical form. In the other

Exocyclica the shell is flattened and the ambitus is oval, or roughly pentagonal (Fig. 152) or heart-shaped (Fig. 153). In these forms the body is lengthened in the antero-posterior axis,* and a distinct bilateral symmetry is apparent; but as in other similar cases amongst Echinoderms this symmetry is delusive, for, when it is closely examined, it is found to be almost entirely confined to the shape of the animal and not to affect the arrangement of the organs.

In these bilateral forms, the mouth may remain central or nearly so (Clypeastroida, Fig. 152), or it may shift towards the anterior edge of the shell in the direction of the anterior radius (Spatangoida, Fig. 153; in the Pourtalesiidae it actually is at the front end on the ambitus). The apical system also, though it remains more or less in the centre of the upper surface, may shift in front of or behind the central point. It thus comes about, as a glance at the figures will show, that the radii and interradii are no longer similar: they differ in length according to the position of the mouth and apical system, as well as in other particulars to be shortly noticed.

In Palaeoecchinoids, Cidaroids, Diadematooids, most Holecypoids and some Spatangoids, the ambulacra are similar throughout their whole course. In Clypeastroids and in most Spatangoids, however, the ambulacral plates present a peculiar modification, described as *petaloid*, on the upper surface. This

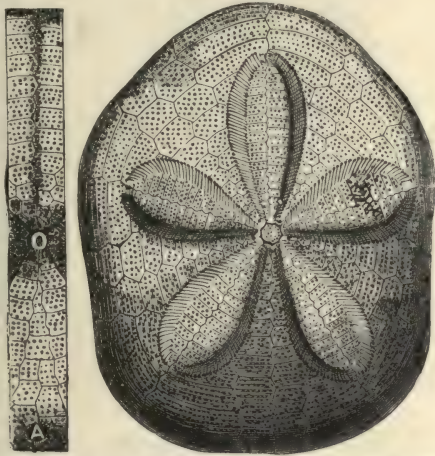


FIG. 152. — *Clypeaster rosaceus* from the aboral side (from Claus). The madreporic plate is in the centre and is surrounded by five genital pores and by the 5-leaved rosette. The anterior radius is directed upwards, and the posterior interradius downward. At the side is the median portion of the oral surface showing the central mouth *O*, and the anus *A* in the posterior interradius.

* The antero-posterior axis is the axis passing through the radius (No. III) to the left of the madreporite which is called the anterior radius, and through the interradius opposite to this, the posterior interradius (No. V. I).

consists in the fact that the ambulacral plates near the apex are narrow, that they gradually become wider as they recede from the apex, and then again become narrow as the ambitus is approached (Figs. 152, 153). The pores of a pair, which are placed near the outer sides of the plates and are connected by grooves (*yoked pores*), accentuate this peculiarity and assist in giving each row of ambulacral plates, in its part next the apex, the appearance of a lanceolate leaf; hence the term *petaloid* which is applied to ambulacra modified in this way. In the

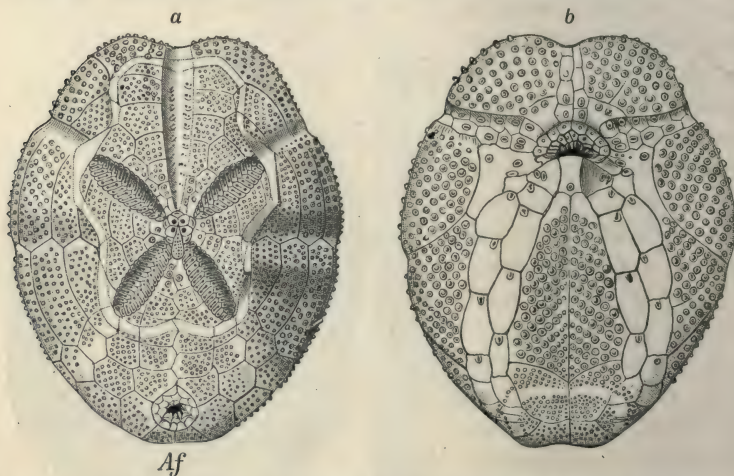


FIG. 153.—Test of an irregular sea-urchin of the Spatangid group, *Brissopsis lyrifera* (from Claus). *a* from the aboral; *b* from the oral side. In *a* the four genital pores are shown (the posterior pore being absent), and the madreporite in the posterior interradius, in which the anus *Af* is also placed; the anterior ambulacrum has not undergone the petaloid modification. In *b* the transversely elongated mouth near the front end, the three short ambulacra of the trivium and the long ambulacra of the bivium are shown, also the fact that the peristomial plates of the interambulacra are single.

Clypeastroids (Fig. 152) all the ambulacra present this modification and constitute a five-leaved rosette, whereas in most Spatangoids, when the modification is present, it is confined to four ambulacra (Fig. 153), the anterior ambulacrum not sharing in it and being different from the rest. The tube-feet issuing from the yoked pores are said to be respiratory * in function.

* This is the view of J. Müller. It is based no doubt upon the double connexion of the foot and its ampulla (p. 232). Inasmuch as the water-vascular system is not distributed to the internal organs and therefore cannot directly be of any use in supplying them with oxygen, it is perhaps permissible to question whether these petaloid feet are correctly described as respiratory. It is possible that they may have some quite different function, e.g. that of sensation.

In the Spatangoids which have petals, the ambulacral plates beyond the petaloid areas are large and the pores consequently at some distance apart (Fig. 153 *b*). Moreover there is a tendency in some species for the pores of a pair to coalesce into one, so that some or all of them are or appear to be single.

In the Clypeastroids there are two kinds of pores: (1) the yoked pores of the petaloid areas which transmit the large respiratory feet, and (2) the minute pores which are single, though by their elongated form they may show signs of being double, and which transmit the locomotive feet (see p. 233). The latter alone are found on the lower surface of the shell (Fig. 155) where they occur on the interambulacral as well as on the ambulacral plates. On the upper side of the shell they are confined

(almost entirely) to the ambulacral plates, and in the petaloid areas to those portions of the ambulacral plates which intervene between the two rows of yoked pores (Fig. 154).

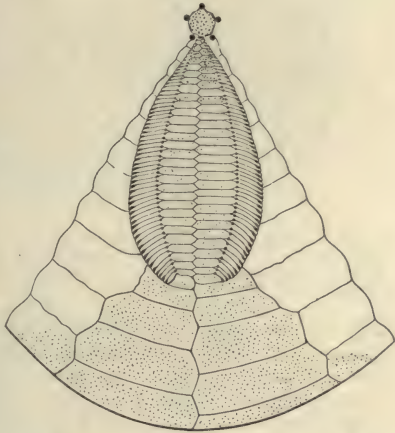


FIG. 154.—Upper side of the anterior radius of *Clypeaster rangianus* Desm., showing the arrangement of the plates and the distribution of the locomotive pores in the region of and beyond the petaloid part of the ambulacrum (after J. Müller).

There are two modes of arrangement of the minute pores. In most Clypeastroids (*Clypeaster*, *Laganum*, *Arachnoides*, *Moulinia*, *Scutellina*, *Echinocyamus*, *Fibularia*, etc.) the pores and feet are distributed over the whole surface of the ambulacra and in some genera extend, on the lower surface of the shell, on to the interambulacra as well; in such Clypeastroids the minute pores were described by Johan. Müller as occurring in **pore-areas**. In the Scutellidae, on the other hand, the minute pores appear to be generally absent in the petaloid areas (except in *Echinarachnius* and *Arachnoides*) and on the lower surface of the shell are arranged along grooves which may branch considerably and extend on to the interambulacral plates (Fig. 157). Sometimes these grooves extend on to the upper surface, but as a general rule they are confined to the lower surface of the shell. These branching tracts of small pores were called by Johannes Müller, their discoverer, **pore-fasciae**. Branches of the radial vessel follow them internally and are connected with the ampullae of the tube-feet which issue from the pores. Similarly in the case of the

pore-areas the lateral branches of the radial canal are long and connected with a number of ampullae and tube-feet (Fig. 155); in the petaloid areas the branches which supply the respiratory tube-feet of the yoked pores supply the locomotive feet as well (Fig. 156). In the petaloid regions

the minute pores are arranged in rows and either perforate the plates or lie along the sutures (the yoked pores being between the plates), while beyond the petals the distribution is irregular. The small pores increase in number with age.

In some genera with diffused pore-areas (e.g. *Arachnoides*) there are grooves (not branched) on the lower side of the shell; they are, however, without pores. It is no doubt the presence of these grooves which has led systematists to place *Arachnoides* with the *Scutellidae*.

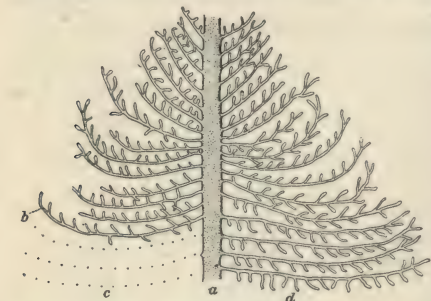


FIG. 155.—Radial vessel from the lower part of an ambulacrum of *Clypeaster placunarius* (after J. Müller). *a* ambulacral canal; *b* lateral branches of the same; *c* pores; *d* ampullae.

ambulatists to place *Arachnoides* with the *Scutellidae*. In many Clypeastroids the ambulacral plates have small internally projecting processes, which may unite with one another to form a kind of internal shell separating a much broken up space, in which the water-vascular canals and the ampullae of the minute feet lie, from the general cavity of the shell. The petaloid ambulacral plates are often sunk below the level of the rest of the test and may serve as brood-cavities or **marsupia**, for the young.

In the Cassidulidae, the lower ends of the ambulacra dilate into petals with crowded tube-feet, arranged round the peristome. These peristomial rosettes are called **phyllodes** (Fig. 173). The interradial marginal plates of the peristome between the phyllodes are slightly protuberant, and the whole figure—inter-radial protuberances and phyllodes—is called the **floscelle**.

In the Exocyclia neither the ambulacral nor the interambulacral plates are continued on to the peristomial membrane, and in the Clypeastroids and Spatangoids the interambulacral part of the peristome is usually constituted of a single plate only.

In the Spatangoida, in which the mouth is in front, the posterior inter-radius is long. The part of it on the lower surface is often protuberant and called the **plastron**. In those Spatangoida with a transversely elongated

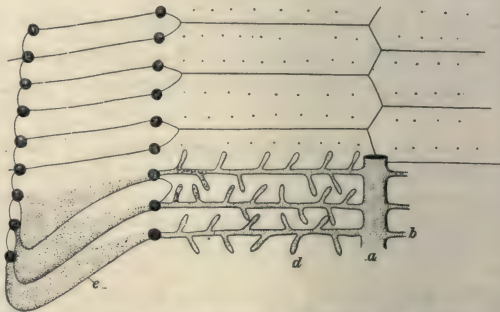


FIG. 156.—Ambulacral plates and vessel from the petaloid region of an old *Clypeaster placunarius* (after J. Müller). *a* radial vessel; *b* its lateral branches; *d* ampullae of locomotive feet, the fine pores of which are shown in the upper part of the figure; *e* ampullae of ambulacral gills.

mouth the marginal plate of the posterior ambulacrum is wide and projecting and called the **labrum** (Fig. 163). The interambulacral plates (or plate) next to the labrum is called the **sternum** (*st*), and the next the episternum (*ep*). When, as happens in most Clypeastroids, the five interambulacral peristomial plates are cut off from the rest of the interambulacral by the widening out of the peristomial end of the ambulacral plates, the interambulacra are said to be **interrupted**.

In the Scutellidae a family of Clypeastroids, the margin of the flattened test may be lobed, or incised at the edge. These incisions are sometimes included in the shell, in which they constitute perforations called **lunulae**. The incisions which are formed during growth, the margin being at first entire, may be very numerous (*Rotula*), or few. The lunulae are always radial, excepting one which occurs in the posterior interradius.

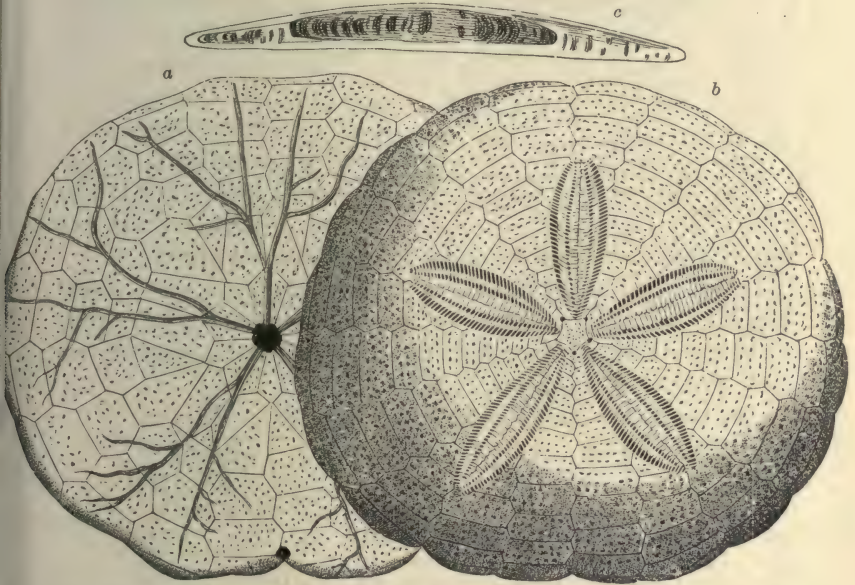


FIG. 157.—*Scutella subrotundata* Lamk. Miocene, Bordeaux (after Zittel), *a* from below; *b* from above; *c* section. Natural size.

The apical system of the Exocyclica is much modified. There is a frequent tendency for the genital opening of the posterior interradius to disappear, and in many Spatangoids the posterior basal plate is also absent. The anal area is occupied either by an extension of the right anterior basal with its madreporitic pores (*ethmophract* condition, *Holactypus*), or the central is said to persist and to fuse with the right anterior basal and posterior basal, the plate so formed being perforated by madreporitic pores (*ethmolysian* condition, many Spatangoids, Fig. 160), or

the radial and basal plates all fuse to form a single plate at the apical pole on which the madreporitic pores are distributed with very

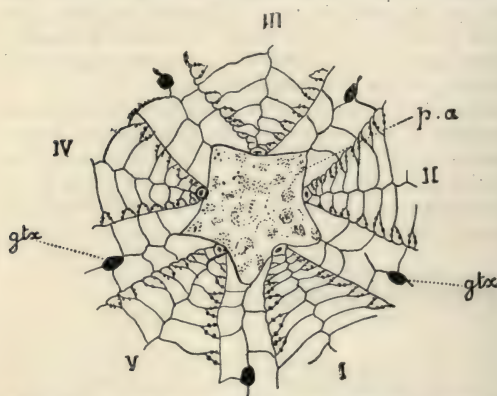


FIG. 159.—*Clypeaster rosaceus* L. apical system and adjacent parts (from Delage after Lovén). The radials and basals are fused to form the single plate *pa* covered with pores, at the apical pole, and the genital openings *gtz* have shifted into the interambulacra, I-V ambulacra numbered.

various arrangement (Clypeastroids, Fig. 159). Further, the madreporitic pores, though typically connected with the right anterior basal, often extend beyond it on to the posterior basal (Fig. 160) or even on to all the basals, and in rare cases beyond the

apical system on the adjacent interambulacral plates.

Lastly in some Clypeastroids the genital openings are found beyond the apical system. In *Clypeaster* itself (Fig. 159) they lie at some little distance from the basals in the interambulacra, and sometimes they are found between the basals and the first interambulacral plates.

It would appear that the association of the genital and water pores with the basal plates is not necessarily a fundamental feature of Echinoid anatomy. In the case of the genital pores this association is undoubtedly not an essential feature, for not only are these pores in some forms dissociated from the basals, as we have just seen, but in the young of all forms which have been examined the basals are not so perforated. The water-pore likewise is sometimes dissociated from the basals in the adult, and in development appears before them. S. Lovén* puts the matter in this way. "The madreporite is not an integral part of the calycinal system, but an extra-neous accessory, and there exists no such thing as a madreporic plate."

In most Holoctypoida the genital aperture of the posterior basal is

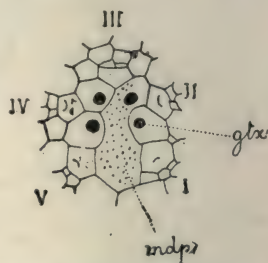


FIG. 160.—Apical system and adjacent parts of young *Spatangus purpureus* showing ethmolysian condition (from Delage after Lovén). *r* radials; *b* basals; *mdp* plate with madreporitic pores formed by fusion of right anterior basal, central plate, and posterior basal; *gtz* genital pore; I-V radii numbered.

* Monograph on *Pourtalesia*, loc. cit., p. 76.

absent, and in *Pygaster* the posterior basal itself is absent. In the Clypeastroids there are usually five genital openings, but sometimes that of the posterior interradius is absent. In Spatangoids there are never more than four genital openings, that of the posterior interradius being absent. In many of the geologically older forms the corresponding basal has also disappeared, but it is present in most recent and living Spatangoids (p. 217), though without a genital opening. In some Spatangoids the genital opening of the right anterior basal is also absent, and

sometimes that of the left anterior as well, so that only two genital openings are left.

In some Spatangoids the apical system presents still more curious variations. The typical arrangement which is found in the Endocyclica and in the Exocyclica described above, and in which the plates are all grouped round a centre, is called **compact**. But in certain Spatangoids it may be **elongated**, i.e. the plates are arranged in two rows extending in an antero-posterior direction (Fig. 161). As a result of this the rays of the trivium are removed by a considerable interval from those of the bivium. This modification is carried still further in the Collyritidae, in which the radials of the bivium are separated, by the junction of the plates of the right and left posterior interradii, from the rest of the apical system (viz. 3 radials and 4 basals, the posterior basal being absent). Such an apical system is said to be **disjunct** (Fig. 162).

Loven's law. In the preceding description of the Echinoid shell, a certain enumeration of the radii and orientation of the shell has been adopted. One of the radii has been called anterior, and one of the interradii posterior, while the three anterior have been spoken of as the trivium and the two posterior as the bivium. When the madreporite is distinct, this orientation can be easily determined; the anterior radius being that to the left of the madreporitic basal (Figs. 148, 161). The orientation is also easy when the anus is outside the apical system, because it

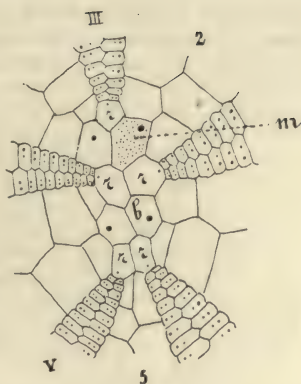


FIG. 161.—Apical system and adjacent parts of *Holaster suborbicularis* Deffr. (after Lovén, from Lang). *m* madreporitic basal; *r* radials; *b* basals; *v* radius *v*; 2 and 5 2nd and 5th interradius.



FIG. 162.—Apical system of *Collyrites elliptica* Lamk. (from Lang, after Lovén). I-V the ambulacra numbered; *a*, *b* the corresponding rows of ambulacra lettered (see Lovén's law).

always lies in the posterior interradius. But in other cases, in which these marks are not so distinct or are not available, the orientation can be determined, as well as confirmed in the preceding cases, by certain

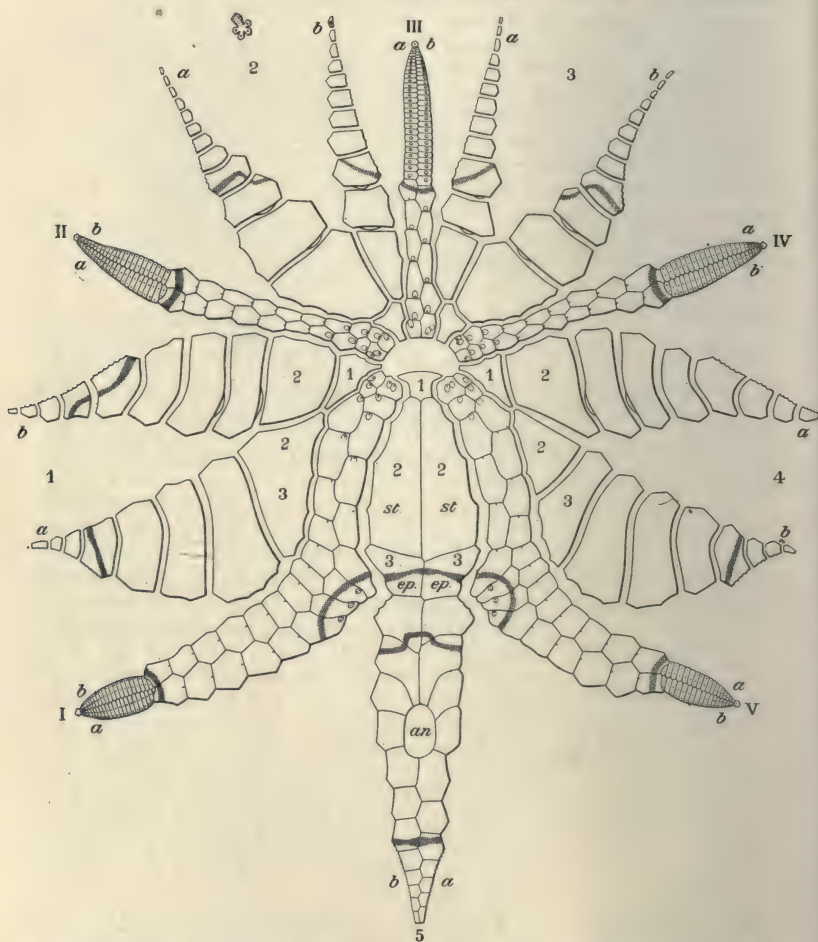


FIG. 163.—*Brissopsis lyrifera* Forb. The plates of the shell spread out and viewed from the oral surface (after Lovén). I to V the radii numbered; 1 to 5 the interradii numbered. In the interradii 1, 4, 5, the three plates next the peristome are numbered to show corresponding plates (note asymmetry in 1 and 4), *a* and *b* mark the rows in each radius and interradius. In interradius 5, 1 marks the plastron and is placed on the labrum, 2 (*st*) the sternum, and 3 (*ep*) the episternum. The apical system is shown in 2, the interradius of the madreporite. *an* anus.

peculiarities of a very remarkable character in the peristomial ambulacral plates. These peculiarities were discovered by Lovén, and the statement of them constitutes Lovén's law. In all Echinoids, except some Pourtalesiidae, the ambulacral plates which border the peristome of the bivium

are, with regard to their size or pores, symmetrical with each other, while the corresponding plates of the trivium are not symmetrical. To particularize further let us take the case of Spatangoids (Fig. 163) : if the shell be viewed from the oral pole and the trivium be directed forward and the bivium backward and the radii be numbered according to the plan used above for Echinoids, viz. in such a way that the right bivial radius (to the left of the observer in this view which is ventral) be numbered I and the left bivial radius V, the other radii being numbered II, III, and IV, and if further the two rows of plates (Fig. 163) in each radius be called *a* and *b*, in such a way that row *a* in radius I is the row next the posterior interradius, and so on all the way round, so that in radius V the row next the posterior interradius is row *b*, then it is found that the ambulacral marginal plates I *a*, II *a*, III *b*, IV *a*, V *b* possess two pores and are larger than the others, viz. I *b*, II *b*, III *a*, IV *b*, V *a*, which also only possess one pore. Further it will be observed that the ambulacral marginal plates of the bivial radii, viz. I and V, are symmetrical with each other, while the corresponding plates in the lateral radii of the trivium, II and IV, are asymmetrical. This law, namely that the marginal ambulacral plates of radii I and V, are symmetrical with each other, while those of radii II and IV are asymmetrical holds for most Echinoidea.

In the regular forms, e.g. *Strongylocentrotus droebachiensis* (Fig. 164), the same law is followed, the difference in the marginal ambulacral plates consisting in their size and in the number of primary plates of which they are composed.

In Clypeastroids Lovén's law is followed only with regard to the size of the plates, and not with regard to the pores, and in some genera its application is very difficult to make out. In the Pourtalesiidae it does not hold at all for the majority of the species, the constitution of the peristome in this family being different from that of other Echinoids. If the law has the importance which Lovén attributes to it, it is most remarkable that in the same family it should hold for some species and not for others.

Pedicellariae * are always present. They have stalks containing a calcareous rod, and three, rarely four, calcified blades (Fig. 166). The bases of the blades are broad and usually concave on the inner side, the concavity being traversed by a vertically directed crest, the *apophysis* (Fig. 167, *a*). The blades are articulated together basally and not with a special calcareous piece. There is a special musculature for moving the blades, and the stalks are movable on the shell. Glands are frequently present on the stalk or on the outer sides of the blades. The pedicellariae are covered with a ciliated epithelium. On the inner sides of the blades patches of this epithelium may be modified as special organs of sense (Fig. 165), the

* Mortensen, *op. cit.*, p. 4. Von Uexküll cited on p. 224. Prouho, *Arch. Zool. Exp. et gén* (2), 5, 1887, p. 213. C. Stewart, *Journ. R. Mic. Soc.* 3, 1880, p. 909.

cells of which are provided with sensory hairs. When these are not present scattered sense-cells are present in the epithelium on the inner sides of the blades. Nerves pass along the stalk

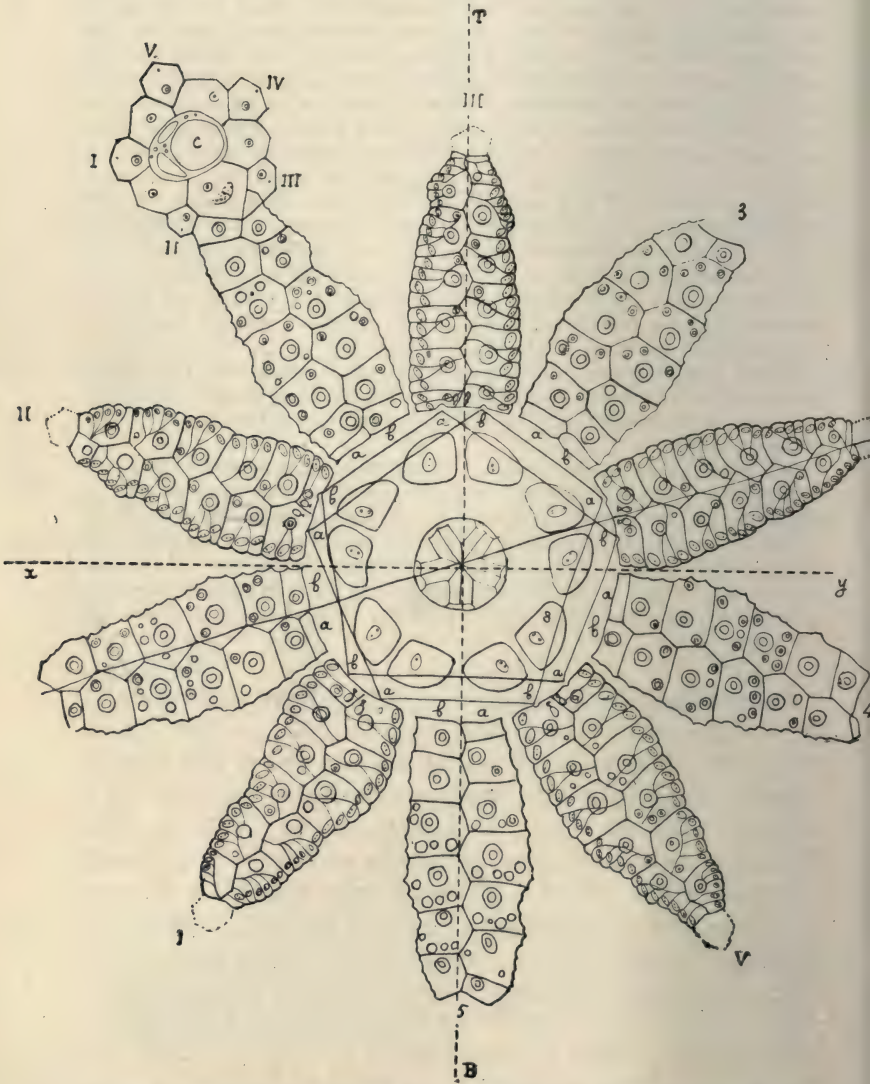


FIG. 164.—*Strongylocentrotus droebachiensis*. The skeleton of a young individual of 4 mm. spread out and viewed from the oral surface. I to V the radii numbered; 1 to 5 the inter-radii numbered; a, b mark the rows in each radius and interradius. The apical system is shown in 2, the interradius of the madreporite (right anterior).

for the innervation of the muscles and sensory epithelium. Pedicellariae are found on all parts of the surface amongst the spines. They are smaller and less numerous in the Irregularia (Spatangoids and Clypeastroids) than in the Regularia. They present considerable variation in structure and are of great importance in classification (Mortensen).

There are four kinds of pedicellariae: the globiferous (gemmiform), the tridentate (tridactyle), the ophicephalous, and the triphylous (trifoliate).

(1) The globiferous pedicellariae (Figs. 165, 167, 1) have long stalks and are provided with a gland, which shows indications of being double, on the outer side of each blade (on the inside in the Cidaridae) and in some cases (*Sphaerechinus granularis*) with three glands half-way up the stalk. The blade ends in a tooth which is grooved on its outer side. The gland of the blade opens on this groove near the tip of the tooth and secretes a viscid fluid which is supposed to be poisonous. There is a patch of sensory epithelium on the inner side of each blade near its base and sometimes a second nearer the apex. The axial calcareous rod extends the whole length of the stalk and the blades are attached to the end of it by a ligament.

The so-called *globifers* are globiferous pedicellariae, the distal parts of which—beyond the stalk-glands—are absent or reduced. They have the form of short stalks ending in a trilobed swelling and have been found in *Sphaerechinus granularis*, *Centrostephanus longispinus*, etc. Traces of blades are sometimes discernible on them.

(2) The tridentate pedicellariae (Figs. 166 C, 167, 4) are the largest and most movable of these organs. Their mobility is due to the fact that the distal end of the stalk is occupied by a rod of elastic tissue embedded in a sheath of smooth muscular fibres, the axial calcareous rod not reaching the whole way. The blades are long, broad at the base and narrow distally, and they are provided with teeth along their edges. They are usually without glands, and the adductor muscles are cross-striped.

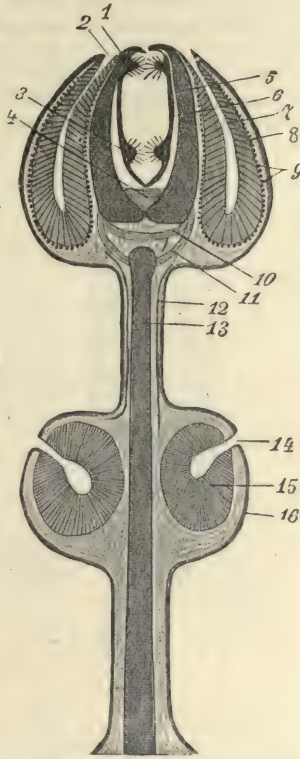


FIG. 165.—Diagram showing the structure of a globiferous pedicellaria (from Lang). 1, 3 sense organs; 2 aperture of the gland of the blade; 4 adductor muscle; 5 skeleton of the blade; 6 epithelium of the blade; 7 gland of the blade, 8 its epithelium; 9 muscle-layer of the gland; 10, 11 divaricator muscles; 12 nerve; 13 calcareous rod of the stalk; 15, 16 gland of the stalk, 14 its aperture.

There are no special organs of sense, but sensory cells are scattered among the ciliated ectoderm cells on the inner sides of the blades.

(3) The ophicephalous pedicellariae, which are distributed all over the shell and on the buccal membrane, are smaller than the preceding. The stalk contains a calcareous rod proximally and an elastic band distally in the axis, and the blades, which are short and broad and toothed along the edges (not shown in the figure), carry at the base a calcareous semicircular rod which crosses those of the two other blades and ensures a good articulation (Fig. 167, 2). The blades are without glands and patches of sensory epithelium, but there are sometimes mucous glands on the stalk in the Diadematae. These glands may be much developed and the blades reduced, in which case they approximate to the *globifer* condition.

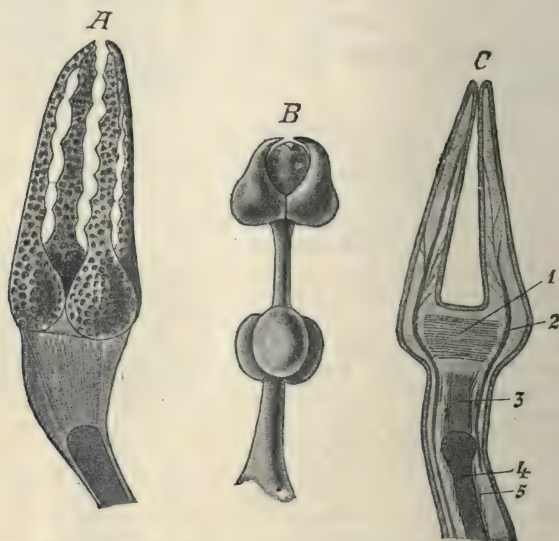


FIG. 166.—Pedicellariae of Echinoids. A, 4-bladed pedicellaria of *Schizaster canaliferus*; B globiferous pedicellaria of *Sphaerechinus granularis* with glands on the stalk; C longitudinal section of a decalcified tridentate pedicellaria of *Centrostephanus longispinus*. 1 adductor muscle; 2 nerve; 3 elastic column; 4 calcareous rod; 5 longitudinal muscular fibre (from Lang).

(4) The triphyllous pedicellariae are the smallest kind and have short broad leaf-like blades without teeth or with very fine teeth (Fig. 167, 4). The stalks are very flexible, the calcareous stalk only reaching half way and being continued by elastic tissue. They are without glands and special sense organs.

The function * of pedicellariae is to seize upon foreign bodies or organisms which approach or touch the shell and spines. The globiferous pedicellariae by means of their poison glands are probably able to deal with the more powerful organisms.

* J. von Uexküll, *Zeitsch. f. Biol.* (2), 19, 1899, p. 334.

In some cases the tube-feet have been observed to transfer to the mouth organisms held by the pedicellariae. The triphyllous pedicellariae are supposed to be particularly concerned in keeping the shell and spines clear of smaller particles such as sand grains which may fall upon them. It is possible that all the pedicellariae may assist in keeping the animals clear of foreign organisms, whether animal or vegetable, which would naturally attach themselves to the spines and shell (see, however, p. 196), thus accounting for the clean condition in which the spiny shell

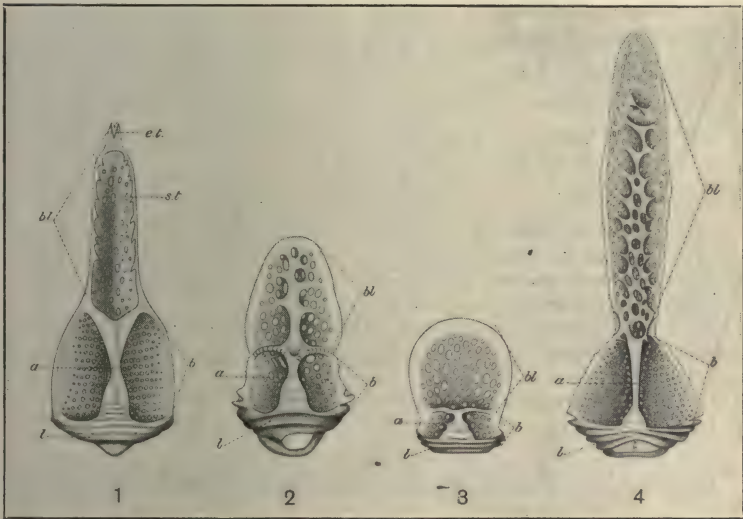


FIG. 167.—Blades of pedicellariae seen from the inner side; 1 of a globiferous (*Parechinus miliaris*), 2 of an ophicephalous (*Strongylocentrotus droebachiensis*), 3 of a triphyllous (*Parechinus miliaris*), 4 of a tridentate pedicellaria (*Strong. droebachiensis*), *a* apophysis; *b* basal part of *bl* blade; *et* end-tooth; *st* lateral tooth; *l* articular surface (after Mortensen).

is usually found. It is said that pedicellariae which have once got hold cannot leave go, so that they must be torn off with the bitten object.

The **spines** are of various sizes and shapes. They are movably articulated to tubercles on the shell plates. The larger tubercles are called primary tubercles and carry the larger or primary spines; they consist of a *mamelon* which may be perforate or imperforate according to the presence or absence of a ligament, and of a *boss* which is the eminence supporting the mamelon; the *scrobicule* is the smooth area of the test round the boss.

The larger spines are attached to their tubercles by an elastic ligament which is inserted into a pit on the tubercle and into another pit in the socket of the spine. The smaller spines are covered by a ciliated epithelium, as are the larger spines in their growing state. The epithelial covering is absent from the full grown larger spines except at their base. The spines are attached by ligamentous and muscular sheaths which pass from the part of the spine round the socket to the smooth part of the shell plate round the tubercle. Around the base of the large spines there is a ring of nervous tissue just beneath the ectoderm.

The large spines * are used in locomotion. The small spines are protective and are arranged round the large spines, and round the pores of the ocular plates, the anal and genital apertures, etc. They can be bent over the protected object, and are without the nerve ring.

In the Clypeastroids and Spatangoids the spines are small and seta-like. In *Asthenosoma* special poison spines have been described by the Sarasins. They have swollen heads containing the poison gland. It is quite possible that the spines are often poisonous.

In *Centrostephanus longispinus* there are about fifteen short spines on the interambulacra near the anus, which are in a continual state of rotation, describing a circle with their tips.

The term **epistroma** is applied to calcareous deposits which are found on the plates of the test in some forms.

Clavulae are minute spines with swollen ends and covered with a ciliated epithelium. They are found in the Spatangoida only and are arranged in definite tracts called **fascioles** or **semities**. The arrangement of these tracts is of importance in classification. The tube-feet within a fasciolar area always differ in structure from those outside it.

The principal kinds of fascioles are as follows (Fig. 168). (1) The peripetalous (*p*), which encloses the petaloid portions of the ambulacra ; (2) the subanal (*sa*), which encloses a space on the oral side of the anus ; (3) the marginal (*m*) along the border of the shell parallel to the ambitus ; (4) the internal (*i*) which crosses the petals near the apical region ; (5) the laterals (*l*), which run one on each side from a point on the peripetalous towards the periproct. They are not all present in the same species.

* For the physiology of the spines see J. v. Uexküll, *Zeit. Biol.* (2), 21, 1899, p. 73, and *ibid.* 22, p. 447.

The structure of the spines affords important systematic characters for the diagnosis of families and to a certain extent of genera.*

Sphaeridia are small, densely calcareous, glassy, spherical bodies, composed of a stratified vitreous substance and placed upon short stalks of which the calcareous tissue is more reticular; the stalks are articulated to prominences on the test. They are found on the ambulacral plates only, and particularly on the ambulacral plates bordering the peristome. They are covered by a ciliated epithelium and round their base is a muscular sheath and a sub-epithelial circular nerve tract—as in the case of the large spines. They may project freely, or be placed in

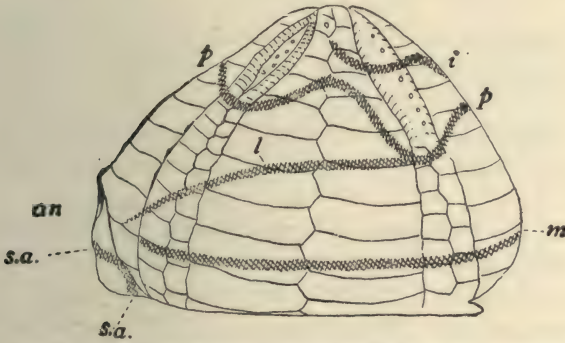


FIG. 168.—Diagram of a Spatangoid showing the fascioles (after Gregory). *i* internal, *l* lateral, *m* marginal, *p* peripetalous, *sa* subanal fasciole.

depressions of the test, which are sometimes completely closed (Clypeastroida, Cassidulidae). They are probably sensory structures, and, from their position near the mouth, they have been supposed to be olfactory or gustatory. On the other hand it has been suggested that they are for orientation. They are to be regarded as modified spines. They are present in all Echinoids except *Cidaris*.

The jaws and five teeth appear to be present in all Echinoids except Spatangoids. In the typical sea-urchins they form the structure known as the *lantern of Aristotle*. The jaws consist of a complicated framework of calcareous plates and rods by means

* E. Hesse, *Neues Jahrb. f. Mineral. Geol. u. Palaeont. Beilageband*, 13, 1889–1901, p. 185.

of which, with the aid of muscles and ligaments, the teeth are brought into action.

The **perignathic girdle**, which is absent in *Spatangoida* consists of processes inwards of the ambulacral and interambulacral peristomial marginal and sometimes adjacent plates. It is said to be **continuous** when the ambulacral processes turn towards one another and unite so as to form an arch—the **auricle**—through which the radial water-vascular canals and nerves, etc., pass. The auricles are connected by the ridges which are processes of the interambulacral plates. The girdle is said to be **interrupted** when the ambulacral processes are absent or very small, while the interambulacral processes are tall and diverge from one another, in such a way as to tend to approximate over the ambulacrum; when they touch and form an arch over the latter, they constitute a false auricle. These processes are for the attachment of the muscles of the jaws. They have been compared to the ambulacral ossicles of Asteroidea.

The body is covered with a ciliated ectoderm, which extends over the smaller spines, the clavulae, sphaeridia and pedicellariae, and on to the bases of the larger spines. Beneath it is the dermis which contains pigment cells and a nerve-plexus, and the plates of the skeleton. Inside the dermis is the ciliated peritoneal epithelium.

Muscles are not present in the body-wall, except in those forms with flexible shell plates in which there are five pairs of longitudinal muscles, running meridionally within the test.

Nervous system.* The arrangement of the ventral nervous system is very similar to that found in Ophiurids. It is removed from the surface, both the circumoral ring and the radial nerves being contained in the epithelial wall of an epineural canal (Fig. 169). It is connected by nerves, which pass through the pores for the tube-feet, with the general sub-epithelial plexus of the ectoderm (7, 8). The epineural canal is developed in the larva by the closure of an ectodermal groove.

The circumoral ring, which is connected with a sub-epithelial or epithelial plexus over part of the intestine, lies between Aristotle's lantern and the peristomial membrane, close to the mouth. The radial trunks lie between the epineural and periaemal canals, and give off nerves to the tube-feet, etc., and as stated above to the integumentary plexus. They end by passing on to

* For the physiology of the nervous system see J. v. Uexküll, *Zeit. Biol.* (2), 21, 1899, p. 73, and 22, p. 447; also the article Echinodermata in the *Cambridge Natural History*, p. 519.

the papilliform termination of the radial water-vascular trunk which perforates each of the ocular plates of the periproct.

The deeper oral system is restricted to five radially-placed patches, close to the circumoral nerve ring, and innervates the muscles of the jaw apparatus. It is absent in Spatangoids.

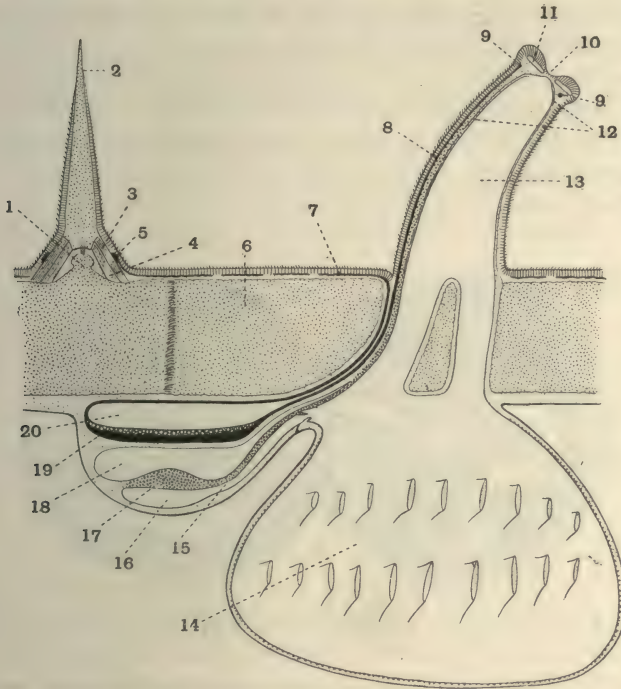


FIG. 169.—Transverse section through a radial part of the body-wall of an Echinoid (diagrammatic after Delage and Hérouard). 1 tubercle for the articulation of 2 a spine; 3 musculus externus, 4 musculus internus of the base of a spine; 5 nerve ring at the base of a spine; 6 ambulacral plate; 7 ectoneural plexus; 8 pedal nerve; 9 nerve ring at the base of a spine; 10 of a tube-foot; 11 skeletal piece in the pedal sucker; 12 muscle of foot; 13 cavity of tube-foot; 14 ampulla traversed by muscular bands; 15 canal passing from radial water-vascular canal, 16 to ampulla; 17 radial blood-strands; 18 radial periaermal canal; 19 radial nerve; 20 epineural canal.

The apical nervous system appears to be unrepresented, unless an annular nerve trunk in connexion with the aboral circular sinus belongs to it.

Sense organs. The tube-feet, and pedicellariae and smaller spines are all highly sensitive and provided in the case of the two latter structures with special aggregations of nervous tissue. The terminal tentacle projects slightly on the ocular plate and

its tip is coloured with pigment ; there is no evidence that it has a visual function. In the *Diadematidae* the skin is provided with numerous shining spots which have the structure of compound eyes (*vide* Sarasin loc. cit.). The sphaeridia have been supposed to have an orientating function.

The **alimentary canal** winds through the body from the mouth to the anus (Fig. 170). It is suspended to the body wall by a perforated mesentery, and sometimes the coils are connected by a mesentery. Pharynx, stomach, intestine and rectum may be distinguished but are little marked off from one another. The junction of the oesophagus and intestine is often marked by a swelling and in *Spatangus* by a caecum. There is an assessor intestine or siphon (absent in *Cidaroida*) which is

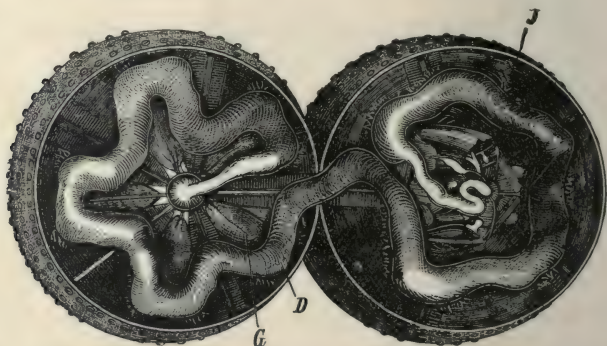


FIG. 170.—Sea-urchin divided equatorially (after Tiedemann, from Claus). *D* alimentary canal, fixed to the shell by the mesentery ; *G* gonads ; *J* interambulacral plates.

given off from it near its commencement (oesophageal region), accompanies it along its inner (axial) wall, and joins it again lower down. It is supposed to allow of the passage of respiratory currents of water. In a few genera (*Schizaster*, *Brissus*, etc.) there is a second siphon. The walls of the alimentary canal contain muscular elements and, in the first part of the intestine at least, blood lacunae. In the *Spatangoida* the alimentary canal is always found distended with sand.

The **coleom** presents essentially the same parts as in *Asteroids*. It consists of water-vascular, perihaemal, and perivisceral portions, and of the axial sinus. The perivisceral portion occupies the greater part of the interior of the body and is in relation with the coils of the alimentary canal.

The **peribaemal** system consists of (1) five radial canals, extending the whole length of the radii and lying between the radial nerve and the radial water-vessel (Fig. 169, 18), and (2) a large sinus round the mouth. This is the **perioesophageal** sinus or lantern-coelom, so called because, in the forms with teeth, the jaws (lantern of Aristotle) lie within it. It is homologous with the outer peribaemal ring of other classes, though it is completely separate in the adult from the radial peribaemal vessels which reach right up to it.

The **external gills**, of which there are five pairs, one pair in each interradius, are processes of the outer part of the peristomial membrane and contain prolongations of this sinus. They pass through notches on the interambulacral marginal plates and are present in most Endocyclica, but are absent in the Cidaroida.

The **internal gills** or Stewart's organs are found in Cidaroida and Echinothuridae. They are hollow processes of the lantern membrane into the body cavity and their cavity is a prolongation of the perioesophageal sinus. They are usually five in number and radial in position. Organs of a similar nature, eight or nine in number, have been described by Cuénot in some Clypeastroids.

The **axial sinus** ends blindly, ventrally, at some distance from the oral region, while dorsally it communicates with the stone-canal. It is contained in the axial organ, which is wrapped round it. There is no inner circumoral peribaemal ring.

There is also an **aboral circular sinus** in the walls of which lies the generative rachis (p. 234). This sinus sends prolongations to the generative organs.

The **water-vascular system** is arranged very much as in Asteroids. There is a circumoral vessel (Fig. 171, *Rg*) placed at the upper end of the pyramids of the jaws and giving off the five radial canals which, passing beneath the intermediate plates, travel oralwards within the lantern-membrane to the test and then, after giving off a branch to the oral tube-feet (absent in *Cidaroida* and *Echinothuridae*) which perforate the plates in the peristomial membrane, turn outwards through the auricles to run along the radii within the shell plates to terminate in the short unpaired tentacle which perforates the ocular plate. In most Endocyclica the circumoral vessel possesses in each interradius

a small outgrowth, which has a spongy structure and has been identified as a polian vesicle; it enters into close relations with branches from the circumoral vascular ring. The radial vessels give off transverse vessels, each of which opens into an ampulla. The ampullae are placed within the shell plates and each of them communicates by two canals with a tube-foot* (Fig. 169). In those cases in which the pores are single, it would appear that the ampulla is only connected by one canal with its tube-foot. The circular vessel is connected by a stone-canal, the walls of

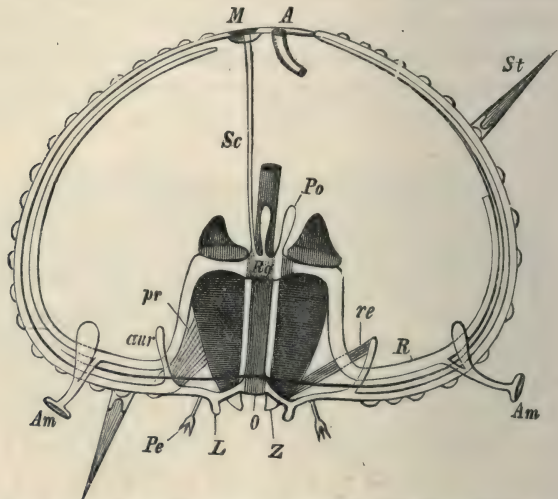


FIG. 171.—Diagram illustrating the relations of the different systems of organs in an *Echinus* (after Huxley). A anus; Am tube-foot; Aur auricle; M madreporite; O mouth; Pe pedicellariae; Po polian vesicle; pr protractor, re retractor muscles of the lantern; R radial vessel of the water-vascular system; Rg circumoral water-vascular vessel; Sc stone-canal; St spine; Z teeth.

which may or may not contain calcareous matter, with an ampulla placed just below the madreporic plate and opening outwards through the pores of this structure. The ampulla communicates with and is really the upper part of the axial sinus, which in Echinoids is surrounded by the axial organ. In *Echinocyamus pusillus* the madreporite is peculiar in the fact that it is pierced by only one water-pore.

In Spatangoids the stone-canal is short and its opening into the axial sinus is separated by a wide interval from the madreporite.

In the Endocyclica the tube-feet terminate in sucking discs and are

* See footnote, p. 214.

supported by calcareous pieces, which form a ring round the margin of the sucker (Fig. 169). In many forms the abactinal tube-feet are pointed and are without the calcareous ring, and in all cases the suckers of the abactinal feet are weaker than the others. The suctional tube-feet together with the spines form the organs of locomotion.

In the Cidaridae and Echinothuridae the feet which come through the ambulacral plates of the peristomial membrane are similar to the other feet. In forms with only ten perforated ambulacral plates on the peristome, the tube-feet which they transmit, the **oral tube-feet** or **buccal tentacles**, are small and terminate in an oval disc. They move actively when in the neighbourhood of food, without, however, touching it. They are supposed to be olfactory or gustatory in function.

In the Clypeastroids and Spatangoids the feet of the petals differ from those of the rest of the ambulacral system. They are broadened at the base, and their sides are indented or sacculated; their walls are without calcareous bodies. They are said to be respiratory in function and are called ambulacral gills (see p. 214).

The tube-feet issuing from the fine pores of Clypeastroids are locomotive. They are cylindrical in form, are provided with calcareous bodies, and end in a sucker (which may be supported by a calcareous ring).

In Spatangoids the feet are very various in shape, according to the part of the body in which they are placed. There are (1) the respiratory feet of the petals without terminal suckers or calcareous bodies; (2) ordinary locomotive feet with suckers and calcareous supports; (3) simple tactile feet without suckers; (4) brush-like tactile feet found round the mouth and the anus and in the Cassidulidae on the phyllodes; they terminate in an expanded disc which carries a number of club-shaped filaments, each of which is supported by a calcareous rod; (5) the rosette-feet of the anterior ambulacrum; these end in discs the edges of which are drawn out into short processes supported by calcareous rods; they are often of great length and are prehensile in function, seizing food which is to be conveyed to the mouth. The feet of the petals are in connexion with double pores in the shell, the other feet only having one pore.

According to J. Müller the locomotive tube-feet of the Spatangoids are less numerous, while those of Clypeastroids are far more numerous, than in regular Echinoids.

The **vascular system** attains a development somewhat similar to that which it has in Holothurians. It consists of a plexus in the intestinal wall connected with two longitudinal intestinal trunks, which lie in the mesenteries. These open into a circumoral vessel* from which pass five radial vessels. The latter lie between the water-vascular canals and the radial periaemal space, and give off vessels to the tube-feet. The circumoral blood-vessel is close to the circumoral water-vascular trunk. As in other cases the significance of this system is obscure: it consists largely of lacunar tissue.

* The word vessel is not perhaps correctly applied to the various tracts and branches of this lacunar tissue.

The **axial organ** is well developed and lies close to the stone-canal in the axial sinus. The dorsal end of it projects into a sinus just below the madreporic plate. This is called the madreporic vesicle, and is the right hydrocoel of the larva. The axial organ consists largely of connective tissue, and, its wall being folded, it appears to be penetrated by epithelial diverticula of the body-cavity on the one hand and the axial sinus on the other. It contains a number of cells which in the larva were derived from a downgrowth into it of the genital rudiment.* Its relation to the axial sinus is described on p. 231.

They are dioecious. The **gonads** are typically five in number ; but in many Spatangoids the number is reduced to 4, 3, or even 2, and in some Clypeastroids to 4. They are branched racemose glands and are interradial in position. With a few exceptions in Clypeastroids, their ducts open through the basal plates.

The genital organs arise as they do in Asteroids as an outgrowth of the genital rudiment (p. 146), which, becoming enclosed by a fold of the wall of the left coelomic sac, encircles the apical pole of the animal and constitutes the genital rachis. The genital organs themselves are developed as outgrowths of the rachis. The part of the left coelom enclosed by the fold above referred to becomes cut off from the rest and persists as the aboral sinus (p. 146).

The eggs are small and very numerous ; they are generally discharged into the sea, where fertilization occurs. In a few forms (species of *Cidaris*) the eggs become attached to the apical part of the test amongst the spines and undergo their development there. In some Spatangoids, some or all of the dorsal parts of the ambulacra are sunk in and serve as brood pouches (marsupia).

The free larva has the pluteus form ; for a description of it and of the main features of the development the reader is referred to pp. 140, 150.

Echinoids have a considerable power of repairing injuries, but not of forming new individuals from broken-off pieces. Asexual reproduction is unknown in the group.

The *Endocyclica* for the most part creep upon a rocky bottom,

* The genital rudiment is developed as a solid outgrowth of the epithelium of the left posterior coelomic sac close to the septum separating it from the left anterior coelom.

and have the power of climbing steep slopes, by means of their powerful suckers. They also use the large spines for locomotion. In the genus *Cidaris*, in which the spines are very large, the feet are not important in locomotion and have feeble suckers. Hence this genus prefers deep water in which it is not rolled about. They frequently live in cavities, which they hollow out of quite hard rock by mechanical action of their teeth or otherwise. The *Exocyclica* on the other hand for the most part live in sand, and the locomotive tube-feet are relatively feebly developed. In *Echinocardium cordatum*, which lives buried about eight inches deep in sand, the tube-feet of the anterior ambulacrum near the apex are very long, several times the length of the animal. They project up through the sand—through a hole above the apex—and end in frilled suckers. They catch food, shrink back through the hole, and hand it to the buccal tentacles.*

There can be little doubt that the affinities of the Echinoidea are with the Asteroids. The general plan of structure and the relations of the chief systems of organs are the same in the two classes. The anatomical differences are small and relate to comparatively unimportant features, such as the structure of the alimentary canal and the calcareous covering of the body. The most important difference is the closure of the ambulacral groove and its conversion into the epineural canal, so that the ectoneural central nervous system is placed in the wall of a closed canal as it is in Chordates, but this peculiarity is shared by Ophiurids. The differences in external form, though considerable at the first glance, are much diminished on a close inspection. If the oro-anal axis of a pentagonal Asteroid such as *Asterina* be elongated and the antambulacral surface reduced we get the body-form of a typical sea-urchin. The madreporite in being aboral and interradiial occupies a similar position in the two classes, and in both Asteroids and regular Echinoids the anus though close to the aboral pole is always slightly excentric. This position of the anus is highly significant not only as indicating the fundamental asymmetry of the body but also because it is identical or nearly identical in the two groups. In Asteroids it is placed in the interradius adjacent to that of the madreporite (Fig. 122); in the regular Echinoids it is either

* An observation of the late Dr. Robertson of Cumbræ communicated by Dr. MacBride.

in this interradius or in the next radius (radius No. I of our enumeration, Fig. 83). In the irregular Echinoids the anus lies in the next interradius but one (interradius No. V. I of our enumeration, Fig. 83)—the so-called posterior interradius of the Exocyclica, and the question arises which position is most primitive, the subapical position in interradius I. II, or in radius I of the Endocyclica, or the position in the Exocyclica in which it lies remote from the apex in interradius V. I. It is impossible to answer this question. On the one hand the similarity between the Asteroids and regular Echinoids on this point suggests that the subapical position is primitive, but this similarity may be apparent only. On the other hand there is plausibility in Lovén's contention that its position in the posterior interradius, recalling as it does the condition found in Palaeozoic Crinoids, is really primitive. Both these arguments, however, rest upon an unproved assumption, viz. that the homologies between the different radii and interradii of the classes of Echinodermata have been determined. We know nothing on this subject, but it must be admitted that, taking into account the obvious affinities between the Asteroids and Echinoids, there is more probability in favour of the homologies implied by the first view than in those implied by the second; for the Crinoids are the most outlying group of living Echinoderms.

The development of Echinoidea, though differing in many points from that of Asteroids, bears out on the whole the view as to their affinities suggested by their adult structure.*

On account of their marine habits and the structure of their body-wall the Echinoidea are well suited for preservation as fossils, and an immense number of extinct species are known. Writing in 1881 A. Agassiz estimated that 2,000 fossil and 225 recent species were known and the number is now probably much greater. The study of these forms and the elucidation of their affinities present problems of the greatest importance to the student of organic evolution. Of the extant families the Cidaridae alone are found in Palaeozoic formations. The Diadematoida, Holoctypoida, Cassidulidae and Collyritidae begin in the Jurassic. The Spatangidae are not found till the Cretaceous, and the Clypeastridae do not make their appearance before the upper

* See MacBride, *Phil. Trans.*, 195, 1903, p. 316.

layers of the Cretaceous. The palaeozoic Palaeoechinoidea are very imperfectly known, but they comprise exocyclic as well as endocyclic forms, though the majority are Endocyclic. They make their appearance in the Upper Cambrian.

From the late appearance of Spatangidae and Clypeastridae it has been commonly assumed that the Endocycilæ preceded the Ectocyclica in evolution. This view is borne out by the fact that *Holætypus* and the Cassidulidae, which are intermediate between the regular and irregular type, preceded the *Spatangidae* in the geological succession. But bearing in mind the fact that *Echinocystites* is an exocyclic form from the Upper Silurian, we should be prudent in suspending our judgment on this point, until the Palaeozoic Echinoid fauna has been more fully investigated—an attitude which is still further justified when we remember that *Collyrites*, which is more modified in some respects in the Spatangid manner than any of the Spatangidae, preceded the latter in its first appearance, and is contemporaneous with (? before) *Holætypus*. tw.

A. Agassiz (*Challenger Echinoids*, p. 19) in discussing the origin of living Echinoids calls attention to the hopeless nature of the attempt to represent the geological succession of forms either diagrammatically or descriptively, and points out that this hopelessness is due to the great number of different combinations of the various characters which have existed in extinct forms. The structural features of living Echinoids are the same essentially as those of extinct forms, but they are combined differently. Features which have apparently disappeared reappear quite suddenly and apparently in no connexion with the types which have immediately preceded them. "We cannot hope," he says, "to trace the development of any type through a series of forms each slightly different from its predecessor; we must only expect to be able to follow the changes of a single feature and study it in its combination with other features, combinations which from their very nature can never form an unbroken series, as their terms are not synchronous."

"If we examine in the same manner [i.e. by tracing it through the Echinoids of all time] any one of the structural features which have once made their appearance, we find that, without exception, they are either persistent to the present day or can be traced in a somewhat modified form in some one of the types now living, though the peculiar combination of any definite number of these may have disappeared."

Finally Agassiz goes on to say (p. 23) that "adopting this method of tracing the development of a single structural feature at a time such as the growth of the poriferous zone from the simple paired zone to the complicated ambulacral zone of a Spatangoid, we shall find that the most primitive ambulacral zone known still exists side by side with the existence at the present day of the resultants, if we may so say, of all the combinations which have taken place."

The classification of the Echinoidea is at present under revision at the hands of Mortensen and others (*op. cit.*). Pending the completion of this work, we have after some hesitation decided to adopt, in its main features, the classification propounded by Duncan (*op. cit.*) in 1891. It has two considerable advantages : it holds the field, having been adopted by Zittel, Delage and Lang in their valuable textbooks ; and it is extremely simple, introducing the smallest possible number of new terms.

The system is as follows :—

Order 1. PALAEECHINOIDEA.

„ 2. EUECHINOIDEA.

Sub-order 1. Cidaroida.

„ 2. Diadematoidea.

Section 1. Streptosomata.

„ 2. Stereosomata.

Sub-order 3. Holecypoida.

„ 4. Clypeastroida.

„ 5. Spatangoida.

Section 1. Asternata.

„ 2. Sternata.

Order 1. PALAEECHINOIDEA.*

With only one or with more than two vertical rows of plates in each of the five interradia, and with two or many vertical rows of simple or compound plates in each of the five ambulacra.

This sub-class comprises exclusively extinct and for the most part palaeozoic † forms. To the characters mentioned in the definition the following may be added. The peristome is in the middle of the oral surface. Jaws are present. The plates may or may not overlap. The anal area is either within the apical system, or outside it in the posterior interambulacrum. *Echinocystites* alone is known to be exocyclic. The sub-class dates from the Upper Cambrian (*Bothriocidaritis*).

The most important genera are as follows :—

Bothriocidaritis Eichw., interambulacral plates in one row, Upper Cambrian. *Echinocystites* W. Thoms., exocyclic, the anus and madreporite

* K. A. Zittel, *Handbuch der Palaeontologie*, Leipzig, 1880 ; also A. Agassiz, *op. cit.*, P. Martin Duncan, *op. cit.*

† *Tiarechinus* is from the Trias, and *Tetracidaritis*, which is here placed with the *Euechinoidea* among the *Cidaridae*, but is by some regarded as belonging to the *Palaeoecchinoidea* is from the Cretaceous.

are on the posterior interradius, interambulacra multiserial, Silurian. *Palaeodiscus* Salter, with flattened body, Silurian. *Lepidocentrus* J. Müll., Devonian. *Koninckocidaris* Dollo and Buis., Carboniferous. *Perischodomus** McCoy, Carb. *Archaeocidaris* McCoy, Carb. *Lepidocidaris* Meek and Worthen, Carb. *Lepidechinus* Hall, Dev., Carb. *Palaeochinus* McCoy, Sil., Carb. *Rhoechinus* W. Keeping, Carb. *Melonites* Norwood and Owen, Carb. *Oligoporus* Meek and Worthen, Carb. *Lepidesthes* Meek and Worthen, Carb. *Tiarechinus* Neumayr, with only four plates in each interambulacrum, one at the peristomium and three extending side by side from the peristomial to the apical system; apical system unusually large.

Order 2. EUECHINOIDEA †

With two vertical rows of plates in each of the five interradii, and a similar number of vertical rows of simple or compound plates in each of the five radii.

The peristome is on the oral side and rarely placed anteriorly towards the edge of the shell. Jaws and teeth are present or absent. The anus is either within the apical system, or in the posterior interradius. The sub-class comprises some extinct and all recent forms. The Cidaroida and Diadematoïda are *Endocyclica* or regular sea-urchins, the Holoctypoida, Clypeastroida and Spatangoida are *Ectocyclica* or irregular forms.

Sub-Order 1. CIDAROIDA.

Test spheroidal. Ambulacra narrow, usually composed of primary plates, rarely compound. Mouth central, anus within the apical system. With internal branchiae only (*Endobranchiata*). With jaws and more or less vertically placed teeth and a discontinuous perignathic girdle. With large spines and tubercles. The interradii as well as the ambulacral plates are continued on to the oral area to the mouth, and are imbricated on the peristome. Sphaeridia, ophecephalous and triphyllous pedicellariae are absent. Carboniferous to the present day; principal distribution in the Jurassic and Cretaceous.

Fam. 1. *Cidaridae* with the characters of the order. *Dorocidaris* A. Ag., N. part of Atlantic Ocean, 50–1,500 fms., *D. papillata* Leske, W. coast Ireland. *Cidaris* Leske, cosmopolitan in the warm seas, littoral to 300 fms. *Phyllacanthus* Brdt., Red Sea to Australia, littoral. *Porocidaris* Desor, *P. purpurata* W. Th., N. Atl., 300–1,500 fms.

Extinct genera: *Orthocidaris* Cotteau, *Temnocidaris* Cotteau, *Diplocidaris* Desor, *Tetracidaris* Cotteau, Cretaceous, see note, p. 238.

Sub-Order 2. DIADEMATOÏDA.

Mouth central, anus within the apical system. ‡ Internal branchiae well developed, reduced, or absent. With external branchiae (*Ectobran-*

* Sollas, *Quart. Journ. Geol. Soc.*, 55, 1899, p. 70.

† P. Martin Duncan, *op. cit.*

‡ In one extinct genus, *Heterodiadema*, the posterior basal is absent, and the periproct is pushed back a slight distance into the posterior interradius.

chiata) and incisions in the peristome margin. With jaws and teeth and continuous perignathic girdle. Ambulacral plates alone continued on to the oral area, where they may appear as separate buccal plates. Sphaeridia, ophicephalous and triphyllous pedicellariae present. Jurassic to the present day.

Section 1. STREPTOSOMATA.

Test more or less flexible, with external and internal branchiae. Peristomial ambulacral plates in several rings.

Fam. **Echinothuridae**. With the characters of the sub-order. The thin and flexible tests are large and tumid, or depressed. Some of the spines of the interambulacra have poison sacs near their ends and are poisonous. The plates of the apical system are usually separate. Coronal plates feebly calcareous and with membranous edge, with open reticulate structure. Internal longitudinal muscles for moving the plates. A flexible echinoid was described in 1863 by S. P. Woodward from the chalk. *Asthenosoma*, the first recent form was described by Grube * in 1868, and rediscovered by Wy. Thomson † in the dredgings of H.M.S. *Porcupine*. The large internal branchiae were discovered by the Sarasin ‡ in 1888.

Pelanechinus Keeping, apical plates absent, Oolitic. *Echinothuria* S. P. Woodward, apical plates absent, Upper Cretaceous; *Phormosoma* Wy. Thoms., recent, 120–2,750 fathoms, N. Atlantic to Azores, in most seas; *Asthenosoma* Gr., recent, 100 to 450 fathoms, N. Atlantic and in most seas. *Echinoma*, *Calveria*, *Araeosoma*, etc.

Section 2. STEREOSOMATA.

Test rigid, with external branchiae, and reduced or absent internal branchiae. With 5 pairs of isolated peristomial ambulacral plates (buccal plates).

Fam. 1. **Saleniidae**. Ectobranchiate, with persistent central or centrals. Ambulacra narrow; the plates are primaries, rarely compound actinally. Interradial plates few, tubercles large. Sphaeridia present. Jaws with the foramina of the pyramids unarched by epiphyses, teeth with a keel. Jurassic to recent. Mostly extinct forms. *Peltastes* Ag., *Acrosalenia* Ag., extinct; *Salenia* Gray, f and r, Caribbean Sea, etc., 60–1,700 fathoms.

Fam. 2. **Hemicidaridae**. Exclusively fossil forms, Permian to Cretaceous. *Hemicidaris* L. Ag., *Acrocidaris* L. Ag., *Goniopygus* L. Ag., genital openings outside the apical system in the interradii; *Circopeltis* Pomel, *Cidaropsis* Cotteau, *Glypticus* L. Ag. *Leptocidaris* Quenstedt, allied here.

Fam. 3. **Aspidodiadematidae**. With spheroidal test and large, narrow, ringed apical system formed by broad basals and broad intervening radials. Interradial plates few. Ambulacra with low primary plates; pores in straight series, one pair in each plate. Peristome incised; branchiae bifid with ten large buccal plates. Tentacles heteropodous. *Aspidodiadema* A. Ag., 100 to 1,700 fathoms, Caribbean Sea, N. part of S. Atlantic, Philippine Sea. *Dermatodiadema* A. Ag.

* *Jahresb. d. Schles. Ges. f. Vaterl. Cult.* 1868, p. 42.

† *Phil. Trans.* 144, 1874, p. 737.

‡ P. and F. Sarasin, *Erg. Nat. For. auf Ceylon*, 1, 1888, p. 129.

Fam. 4. **Diademataidae**. Regular, ectobranchiate, with or without vestiges of internal branchiae; shell highly ornamented; ambulacra usually narrower than interambulacra, with vertical rows of primary tubercles, and usually consisting of compound plates, all the components of which are primaries; the pore-pairs are usually in a simple row, and sometimes in double rows only near the mouth and apex. Interambulacra also with vertical rows of primary tubercles. Teeth grooved, jaws without a closed pyramidal foramen, feet heteropodous. Chief distribution in Jurassic, Chalk and Tertiary.

Diadema Schynvoet, with blue patches (ocellar) on the shell, f and r, most seas; *Centrostephanus* Ptrs., r; *Placodiadema* Duncan, f; *Heterodiadema* Cotteau, f; *Codiopsis* L. Ag., f; *Pleurodiadema* De Loriol, f; *Magnosia* Michelin, f; *Cottaldia* Desor, f; *Diplopodia* McCoy, f; *Pedinopsis* Cotteau, f; *Acanthechinus* Duncan and Sladen, f; *Phymechinus* Desor, f; *Asteropsis* Cotteau, f; *Diplotagma* Schlüter, f; *Micropyga* A. Ag., r, 100 to 600 fathoms, Philippines, Fiji; *Plistophyma* Péron and Gauthier, f; *Pedina* L. Ag., f; *Echinopedina* Cotteau, f; *Stomechinus* Desor, f; *Micropedina* Cotteau, f; *Heterocidaris* Cotteau, f; *Echinothrix* Peters, r, East coast Africa, Pacific Islands, Red Sea, etc.; *Astropyga* Gray, r, Panama, California, Zanzibar, etc., with overlapping plates; *Polycephus* L. Ag., f; *Codechinus* Desor, f; *Orthopsis* Cotteau, f; *Eodiadema* Duncan, f; *Péronia* Duncan, f; *Echinopsis* L. Ag., f; *Gymnodiadema* De Loriol, f. *Progonechinus* Duncan and Sladen, f, allied here.

Fam. 5. **Cyphosomatidae**. Contains only one recent genus, *Coptosoma* Desor, f and r; and the following extinct genera. *Cyphosoma* L. Ag., *Gauthieria* Lambert, *Thylechinus* Pomel, *Micropsis* Cotteau.

Fam. 6. **Arbaciidae**. Test depressed abactinally, flat actinally; epistroma with granules, projecting ridges, sessile glassy knobs. Apical system large; periproct oval and oblique, composed of four triangular plates; pore in ocular plates double. Ambulacra straight, narrow, expanding near the peristome; pore-pairs simple or in large arcs or crowded actinally; plates compound near the ambitus; in the compound plates the middle component is a large primary, while the aboral and adoral components are demiplates, or the primary is adoral and the demiplates are aboral to it. Sphaeridia solitary or numerous. Peristome large, incurved at the sides of the ambulacra. Teeth keeled; auricles not closed above. Tertiary and recent. *Arbacia* Gray, f and r; *Echinocidaris* Duncan and Sladen, r, most seas; *Coelopleurus* L. Ag., f and r; *Podocidaris* A. Ag., r, 150 to 1,075 fms., Caribbean, Philippines; *Dialithocidaris* A. Ag., deep sea.

Fam. 7. **Temnopleuridae**. Regular ectobranchiate with the teeth keeled, and auricles closed. Ambulacra with triple compound plates. The suture of the ambulacral and interradiial plates and of the apical system grooved and may be pitted, or there may be a raised ornamentation, costulate or reticulate or in ridges, the sutures being furrowed or not. Cretaceous to recent. *Glyphocyphus* J. Haime, f; *Dictyopleurus* Duncan and Sladen, f; *Arachniopleurus* Dun. and Slad., f; *Ortholophus* Duncan, f; *Paradoxechinus* Laube, f; *Echinocyphus* Cotteau, f; *Zeuglopleurus* Gregory, f; *Lepidopleurus* Dun. and Slad., f; *Coptophyma* Péron and Gauthier, f; *Trigonocidaris* A. Ag., r, Florida, Caribbean, etc.; *Temnopleurus* L. Ag., f and r, Indian Ocean, Persian Gulf, Pacific; *Pleurechinus* L. Ag., f and r; *Temnechinus* Forbes, f and r; *Salmacis* L. Ag., f and r, Red Sea, Ind. Ocean, etc.; *Salmacopsis* Döderlein, r; *Mespilia* Desor,

r; *Microcyphus* L. Ag., r; *Amblypneustes* L. Ag., r; *Goniopneustes* Duncan, r; *Holopneustes* L. Ag., r; *Hypsiechinus* Mrtsn., r; *Grammechinus* Dun. and Slad., f.

Fam. 8. **Stomopneustidae.** Large forms with closed auricles and powerful spines. Globiferous pedicellariae without end-tooth. *Stomopneustes* L. Ag., littoral, Indian Ocean, Australia.

Fam. 9. **Echinidae.** Regular shell with ambulacra and interambulacra of equal width; tube feet similar. Ambulacral plates compound with three pairs of pores which are arranged in arches of triplets. Peristomial notches small. Coronal plates without pits or grooves, and their opposed surfaces are plain. Globiferous ped. with an end-tooth and one or several lateral teeth on each side. Teeth keeled. Cretaceous to recent. *Parachinus* Mrtsn., pores trigeminate, primary tubercle on all the ambulacral plates, globiferous pedicellariae without neck and no cross beams connect the edges across the inside of the blade, numerous short greenish spines; *P. miliaris* Müll., North Sea, etc. *Loxechinus* Des. *Echinus* L., pores trigeminate, primary tubercle on every or only on every other ambulacral plate, spines upon the whole long and strong, the actual primary spines not curved at the point, globiferous pedicellariae generally with the edges connected across the inside of the blade, no ocular plate reaches to the periproct. *E. esculentus* L., primary spines short, mainly littoral to about 100 fms. *E. acutus* Lmk., primary spines much longer than secondary, to 1,350 fms. *Sterechinus* Koehler, *Paracentrotus* Mrtsn., *P. lividus*. Fossil genera, *Stirechinus*, *Glyptechinus*, *Sporotaxis*, etc.

Fam. 10. **Toxopneustidae.** Globiferous pedicellariae with end-tooth but without lateral teeth, the edges of the blade quite coalesced on the inside so that the blade is tubular, usually 1-2 oculars reach the periproct. *Psammechinus* L. Ag. *Gymnechinus* Mrtsn. *Toxopneustes* L. Ag. (*Boletia* Des.), littoral forms, Ind.-Pacific Oc. *Tripneustes* Ag. *Sphaerechinus* Des., Channel Islands, Med., etc. *Pseudoboletia* Trosch. *Pseudocentrotus* Mrtsn. *Strongylocentrotus* Brdt., *S. droebachiensis* Müll. *Antho- cidaris* Ltk. *Parasalenia* A. Ag.

Fam. 11. **Echinometridae.** Globiferous pedicellariae with end-tooth and one unpaired, strong lateral tooth, the edges of the blade almost always connected by cross-beams across the inside; no neck; all littoral. *Pseudechinus* Mrtsn. *Heliocidaris* Desml. (*Evechinus* Ver.), New Zealand. *Echinostrephus* Ag., Indo-Pac. *Toxocidaris* Ag., Australia. *Echinometra* Rond., cosmop. in warm zone. *Heterocentrotus* Brdt., Indo-Pac. *Colobocentrotus* Brdt., Indo-Pac.

Sub-Order 3. HOLECTYPOIDA.

Mouth central, anus outside the apical system in the posterior inter-radius, either dorsal and close to the apical system (*Pygaster*, *Pygastrides*) or ventral (*Holectypus*, etc.). The posterior genital opening usually absent. The madreporite may extend back and occupy the place of the anal area. With external branchiae, apetaloid ambulacra, and a pair of pores or only one pore on each ambulacral plate. The plates of the corona are not prolonged on to the peristome. With feeble jaws and vertical teeth, or without these structures. Sphaeridia present. The perignathic girdle is variable: it may be weak, or it may form a strong collar, the interradian portions of it being wide and bent upwards and outwards from the peristome internally. All the genera included in this group are Jurassic and

Cretaceous, except *Pygastrides* * Lovén from the Caribbean Sea, 200-300 fathoms. The fossil genera are *Holactypus* Desor, *Pileus* Desor, *Pygaster* L. Ag., without the posterior basal; *Discoidea* Klein; *Conoclypeus* L. Ag. *Galeropygus* Cotteau is allied here.

Sub-Order 4. **CLYPEASTROIDA** (Cake-urchins).

Mouth central or nearly so; anus outside the apical system in the posterior interradius and is either on the lower side or at the margin. With external branchiae and well-developed jaws and jaw skeleton. Tube-feet heteropodous. The edge of the corona is usually close to the mouth and there are no perforated ambulacral plates in the peristomial membrane. Peristomial margin consists of 10 ambulacral † and usually 5 interambulacral plates. Teeth usually more or less horizontal, rarely vertical. Sphaeridia are present, few, and covered. The test is usually flat, rarely arched dorsally; its margin may be notched. Its cavity is traversed by calcareous pillars and septa which pass from its upper to its lower walls. The apical system is much reduced. The madreporite is central (Fig. 159) and the basal plates are coalesced with each other and sometimes with the oculars. The madreporite may spread out on to all the apical plates, and the generative openings may descend into the interambulacral areas (p. 218). There are at least four genital openings, usually five; when only four the posterior is absent. There are five petals (Fig. 152) with pairs of pores, which pass out between the plates and are generally yoked. There are numerous small simple tube-feet, each one in relation with one pore; for the arrangement of these see p. 215. The interambulacral plates may be interrupted (p. 217) and often have small single pores, at least on the lower surface of the shell. The interambulacral marginal peristomial plates are single; the perignathic girdle is discontinuous. In the young state the shell is regular and there are five equal interradii. Cretaceous to the present day.

Fam. 1. **Fibulariidae**. Small forms with rudimentary, widely open, few-pored petals, pores of petals not yoked; jaws rather high, teeth superior and slanting. Perignathic processes broad, low, one on each interradius. Interambulacra small, terminating in a single apical and a single peristomial plate. Periproct usually on the lower surface. Slightly developed vertical partitions within the test, limiting the ambulacra at their side on the oral surface and radiating towards the peristome. A sphaeridium in each ambulacrum, covered. *Echinocyamus* van Phels., f and r, madreporite with only one pore, pore-pairs not yoked. *E. pusillus* Gray, N.E. Atlantic and Brit. Seas, Mediterranean, etc.; *Sismondia* Desor, Runa A. Ag.; *Fibularia* Lamk. r and f; *Moulinsia* L. Ag.; *Rotuloidea* R. Etheridge.

Fam. 2. **Clypeastridae**. Petals well developed; usually unequal; actinal furrows straight. Small pores scattered, generally on interambulacra as well as on ambulacra and not specially confined to furrows. Interambulacra actinally discontinuous, one peristomial and two apical plates in each. Sphaeridia, two in each ambulacrum, covered. Perignathic

* Lovén, *Bih. Svenske Akad. Hand.*, 13, 1888.

† In some Clypeastroids two small tube-feet, each with a separate pore, perforate the edge of each pair of marginal ambulacral plates (J. Müller, *op. cit.*, p. 39). These seem to be the only representatives of the marked oral tube-feet of Spatangoids.

processes tall, narrow, two on each ambulacrum, fitting in below the jaws. Genital pores sometimes outside the apical system (see p. 218).

Clypeaster Lamk. (Fig. 172), Red Sea, Indian Ocean and warmer seas generally; *Diplothicanthus* Duncan, *Plesianthus* Duncan, all recent and

fossil; *Anomalanthus* J. Bell, r.

Fam. 3. **Laganidae.** Test flat; petals unequal, narrow, lanceolate; ambulacra beyond them very wide; pore-pairs for branchial tube-feet few, and between them are minute pores for prehensile tentacles. Interradii small, continuous; each with a single apical and peristomial plate. Periproct between the peristome and posterior margin. Perignathic processes single on the interradial peristomial plates, situated so as to be beyond not below the jaws. *Laganum* Klein, r and f.

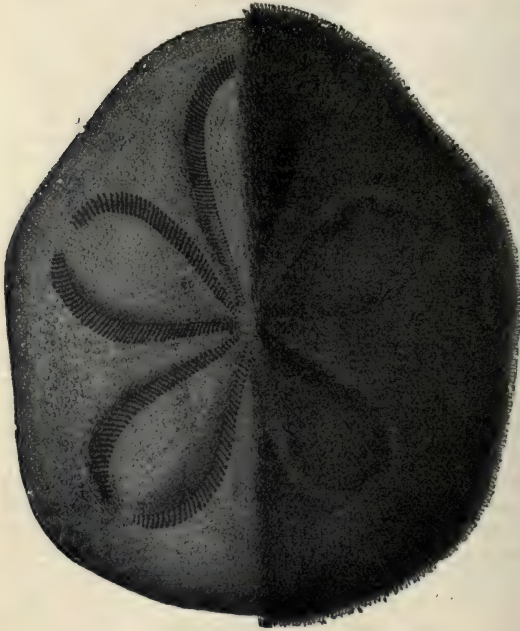


FIG. 172.—*Clypeaster rosaceus* (Règne animal).

lidae. Test very flat, often lobed or perforated. Ambulacral furrows on lower side bifurcating and branching (*pore-fasciae*); small pores on actinal surface only found in furrows. Radiating partitions internally. *Scutella* Lamk. (Fig. 157), fossil; *Echinarachnius* Leske, r; *Echinodiscus* Breynius, f and r; *Encope* L. Ag., f and r; *Mellita* Klein, f and r; *Lenita* Desor, f; *Mortonia* Desor, f; *Rotula* Klein, r; *Arachnoides* Breynius, f and r.

Sub-Order 5. **SPATANGOIDA** (Heart-urchins).

Test often more or less heart-shaped. Mouth central or subcentral, or at the front end of the lower surface of the shell. Anus outside the apical system in the posterior interradius (Fig. 153). External gills, jaws, teeth and perignathous ring absent. The plates of the shell are not continued on to the peristome. Sphaeridia present. Large spines are never found. Fascioles and clavulae are frequently present. There is usually an ambulacral rosette on the upper surface; sometimes with only four petals, the anterior ambulacrum not being petaloid.

When the mouth is shifted in the direction of the anterior radius, it is transversely elongated and possesses on its hinder border a lip formed by

the enlarged peristomial plate (**labrum**) of the posterior interradius. They are usually sand-burrowers and the tube-feet show considerable diversity.

In the young state the form approaches that of the regular urchins in the position of the mouth and the form of the ambulacra. Jurassic to the present time. The Spatangidae are first found in the Cretaceous.

Section 1. ASTERNATA.

Shell oval, mouth central or sub-central, without sternum and fascioles; ambulacra all alike, simple or petaloid. Apical system compact or elongate. Interradii some or all with a single peristomial plate. Without plastrons, with or without floscelles. Through the Echinoneidae they are related to the regular forms and through the Cassidulidae to the Clypeastrids.

Fam. 1. **Echinoneidae**. Ambulacra simple, all alike, without petals. Mouth central, without floscelle. With four perforated basal plates. Mostly begin in Cretaceous, but a few in the Jurassic. *Echinoconus* Breyn., f, Cretaceous; *Lanieria* Duncan, f; *Echinoneus* van Phel., f and r, Caribbean Sea, Australia, Zanzibar, etc.; *Amblypygus* L. Ag., f; *Caratomus* L. Ag., f; *Pygaulus* L. Ag., f; *Pyrina* Desm., f, Jurassic to Eocene; *Nucleopygus* L. Ag., f; *Anorthopygus* Cotteau, f; *Haimea* Mich. f; *Oligopygus* De Lor., f; *Echinobrissus* Breyn. (*Nucleolites* Lm.), f; *Anochanus* Grube, r; *Botriopygus* d'Orb. f; *Ilariona* Dames, f.

Fam. 2. **Cassidulidae**. Ambulacra petaloid or not, closed or open below. Peristome with floscelle (Fig. 173). With four genital pores, the basals are sometimes fused; the madreporite much extended. Jurassic to present day. *Cassidulus* Lamk., f; *Echinanthus* Breyn., f; *Studeria* Dunc. (*Catopygus* L. Ag.), f and r; *Clypeus* Klein, f; *Pygurus* d'Orb., f; *Echinolampas* Gray, f and r; *Conolampas* A. Ag. r; *Neolampas* A. Ag., r; *Rhynchopygus* d'Orb., r.

Section 2. STERNATA.

Peristome excentric anteriorly. Sternum well developed. Anterior ambulacrum different from the rest (except in Anachytidae). Fascioles present or absent. Without floscelle.

Fam. 1. **Collyritidae**. Without floscelle; apical system elongate (Fig. 162), disjunct; the two posterior radials being separated by a con-

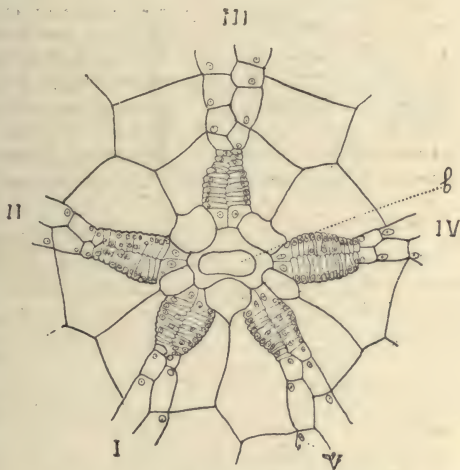


FIG. 173.—Oral region of *Cassidulus pacificus* showing phyllodes (after Lovén from Delage). *b* mouth; I-V radii numbered.

siderable interval, which is occupied by supplementary plates, from the rest of the apical system. Ambulaera similar, Jurassic, Cretaceous. All fossil. *Dysaster* L. Ag.; *Collyrites* Desm.

Fam. 2. **Plesiospatangidae.** Fossil.

Fam. 3. **Ananchytidae.** Apical system elongate or compact. Apetalous. With or without an anterior groove. *Echinocorys* Breyn., f; *Holaster* L. Ag. (Fig. 161), f; *Offaster* Desor, f; *Cardiaster* Forbes, f; *Urechinus* A. Ag., 422–1,800 fathoms, Pacific; *Cystechinus* A. Ag., f and r; 1,000–2,000 fathoms; *Calymne* W. Thoms., r, 2,650 fathoms, N. of Bermuda.

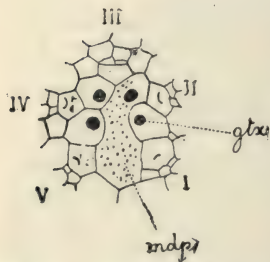


FIG. 174.—Apical region of *Spatangus purpureus* (after Lovén from Delage). *gtx* basal; *mdp* madreporite; I–V radii numbered.

Fam. 4. **Spatangidae.** Usually heart-shaped and with an anterior groove. Apical system with four or less perforated plates; compact or with the madreporite variable in its posterior extension; radials five and external. The test is longer than broad and bilateral symmetry is marked. The anterior ambulacrum is always different from the other four, which may be petaloid abactinally. Fascioles are present in most genera, but they may be absent; and the genera may be grouped according to this

feature and their arrangement if present. They begin in the Lower Cretaceous, and reach their highest development at the present day.

Recent Genera.

Platybrissus Grube; *Palaeopneustes* A. Ag., Caribbean Sea; *Hemiaster* Desor, f and r; *Faorina* Gray, China; *Linthia* Merian, f and r; *Schizaster* L. Ag., f and r; *Agassizia* Val., f and r; *Moiria* A. Ag., f and r; *Moiropsis* A. Ag.; *Brisus* Klein, f and r; *Meoma* Gray, f and r; *Metalia* Gray, f and r; *Rhinobrisus* A. Ag.; *Brisopsis* L. Ag., f and r; *Spatangus* Klein, f and r, *S. purpureus* Leske, 5–530 fms., Channel Islands, North Sea, etc.; *Maretia* Gray, f and r, 25 to 800 fathoms; *Eupa-*

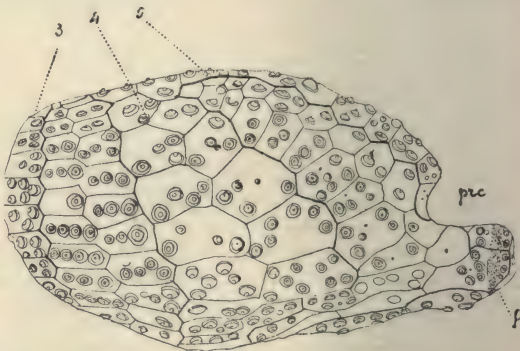


FIG. 175.—*Pourtalesia jeffreysi* (from Delage, after Lovén). *f* anal semite; *prc* periproct; 3, 4, 5 third, fourth and fifth interradial.

tagus L. Ag., f and r, Australia; *Macropneustes* L. Ag., f and r, Caribbean; *Nacospatangus* A. Ag., *Linopneustes* A. Ag.; *Cionobrisus* A. Ag.; *Echinocardium* Gray, f and r, littoral to 2,675 fathoms, worldwide; *Breynia* Desor, f and r; *Lovenia* L. Ag. and Desor, f and r, 10–28 fathoms.

The following are apetalous: *Genicopatagus* A. Ag., Antarctic; *Palaeo-*

brissus A. Ag., Caribbean; *Aceste* W. Thom., 600 to 2,600 fathoms; *Aerope* W. Thom., 800 to 1,750 fathoms; *Palaeotropus* Lovén, 82 to 375 fms.; *Homolampas* A. Ag., 32 to 2,475 fms.; *Argopatus* A. Ag., 800 fms.

Fam. 3. **Leskiidae**. Test thin, ovoid. Apical system with three basals fused into one; two large genital pores upon conical prominences. Peristome in front, pentagonal, with five angular buccal plates. A peripetalous fasciole. *Palaeostoma* Lovén, China.

Fam. 4. **Pourtalesiidae**. Elongated and Holothurian-like in appearance. Test thin, transparent. Mouth terminal in front. Anus behind, above the posterior projecting rostrum if that is present, or terminal on the actinal surface. Apical system variable, compact or disjunct. Peristomial margin also variable: in some species Lovén's law is carried out, in others it is not. Ambulacra not petaloid. With four or three genital openings. Plates for the most part with single pores; tube-feet homoiopodous. Is the living representative of the Cretaceous genus *Infulaster* Hag. Atlantic and Pacific, 345 to 3,000 fms.

Pourtalesia A. Ag., *Spatagocystis* A. Ag., *Echinocrepis* A. Ag.

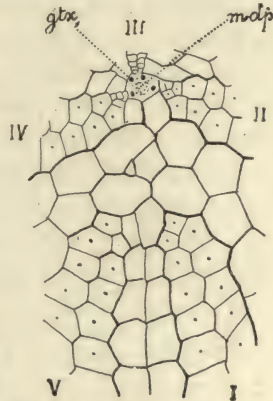


FIG. 176.—Apical region of *Pourtalesia jeffreysi* (after Lovén, from Delage). *gtz* genital opening; *mdp* madreporite.

Class HOLOTHUROIDEA.* Sea-cucumbers.

Elongated, worm-like Echinoderms with a dermo-muscular body wall containing small isolated calcareous bodies. With contractile tentacles surrounding the mouth and containing prolongations of the water-vascular system. The apical system of plates is not developed at any stage of life, and the water-vascular pore

* J. Müller, *Ueb. Synapta digitata u. üb. die Erzeugung von Schnecken in Holothuriën*, Berlin, 1852. G. F. Jaeger, *De Holothuriis*. Diss. Inaug. Zurich, 1833. De Quatrefages, *Mém. sur la Synapte de Duvernoy*, Ann. Sci. Nat. (2), 17, 1842. A. Baur, *Beit. z. Naturgesch. d. Synapta digitata*, Dresden, 1864, and Jena, 1865. Semper, *Holothuriën, Reisen in Archipel der Philippinen*, II. 1, 1868. H. Ludwig, "The Holothuroidea," *Mem. of the Museum of Comp. Zoology Harvard College*, vol. 17, 1894. *Id.* "Holothuroidea" in Bronn's *Klassen und Ordnungen des Thierreichs*, Bd. 2, Abt. 3, 1889–1892. Theel, H., "Report on the Holothuroidea," *Challenger Reports*, Pt. 1, in vol. 4, 1882, and Pt. 2, in vol. 14, 1886. *Id.*, "Report on the Holothuroidea," *Bull. Mus. Com. Zool. Harvard College*, 13, 1886. R. Perrier, *Holothuries, Exped. Sc. Travailleur et Talisman*, 2, 1902, p. 273. A. Kowalevsky, *Beit. z. Ent. d. Holothuriën*, Petersburg, 1867. R. Semon, *Entwick. d. Synapta*, Jena. Zeitschrift, 22, 1888, p. 175. H. Ludwig, *Zur Entwick. der Holothuriën (Cucumaria planci)*, Sitzber. k. Preuss. Acad. d. Wiss. Berlin, 1891. E. Hérouard, *Recherches sur les Holothuries des côtes de France*, Arch. Zool. Exp. (2), 7, 1889, p. 555, and *Holothuries provenant des campagnes de la "Princesse Alice," Rés. camp. sc. Monaco*, Fasc. 21, 1902. Romanes and Ewart, *Observations on the locomotor system of Echinodermata*, Phil. Trans., 1882, p. 829.

is usually absent in the adult. The axial organ and generative rachis are not present.

In the Holothurians or sea-cucumbers the body is elongated in the direction of the long axis, at or near the two ends of which are the mouth and anus respectively, and the radial water-vessels are disposed in five equidistant meridional rows, extending from the oral to the anal pole. The mouth is surrounded by a row of tentacles and the animal lies with its long axis parallel to



FIG. 177. *Cucumaria* with extended dendritically branched tentacles *T*. *Af* tube-feet (from Claus).

the substratum. Typically the mouth and anus are terminal, and there are five usually double rows of tube-feet which mark the radii and pass from the oral to the anal end of the body (Fig. 177). In such cases the symmetry is pentamerous and there is apparently nothing to mark one side of the body from the other. But as a matter of fact there are two structures which are not radially disposed. These are the stone-canal and the generative opening. The generative opening, which is single, is placed in the centre of an interradius, usually not far behind the tentacular circle, and the stone-canal is in the middle line of the same interradius.

This interradius is called dorsal. It enables us to distinguish a ventral radius, a right and left ventral radius, and a right and left dorsal radius. Our enumeration of the radii of Holothurians (Fig. 182) is the same as that adopted for other classes. It is based on the assumption that the madreporitic interradius is the same in all cases. We need not repeat our warning (p. 119) as to the inadvisability of basing important speculations as to homologies on this assumption. It sometimes

happens that the side of the body carrying the three ventral radii and two ventral interradii (trivium) is flattened and modified into a sole-like creeping surface (Fig. 185), while the dorsal side with its two dorsal radii (bivium) and three interradii is arched. In such cases the tube-feet of the trivium have discoidal ends and are suctional in function, while those of the bivium are pointed and probably have a respiratory or tactile function: such non-locomotory pointed tube-feet are called **ambulacral papillae**. It will be noted that the radii of the bivium are not the same as in Asteroids and Echinoids (Fig. 182, cf. with Fig. 83).

The body may be circular, or pentagonal in section; when pentagonal the radii occupy the angles. More rarely the body is flask-shaped (*Rhopalodina*) or spherical. The ventral sole may occupy the whole length of the animal (*Colochirus*, *Stichopus*, *Mülleria* etc.), or be confined to the middle portion (*Psolus*, *Psolidium*). Sometimes the dorsal interradius is much shortened (*Ypsilothuria*) and concave, the ventral surface being correspondingly elongated and convex. In such cases the oral and aboral poles are approximated. In *Rhopalodina* this modification is carried to an extreme in that the dorsal interradius is practically obliterated. In this case the body is flask-shaped, the mouth and anus being closely approximated, with the genital opening between them, at the end of the neck of the flask, and the body appears to have ten radii. In other cases the two ends of the long axis are bent ventralwards so that the mouth and anus appear to be on the ventral surface at each end of the flattened sole-like surface. Finally in certain deep-sea forms processes may be developed from the dorsal surface of the body. In *Psychropotes* the hinder region of the body projects back over the anus (Fig. 185), and in *Pentagone* dorsal lobes are developed over the anterior part of the body. In the pelagic form *Pelagothuria* (Fig. 186) a kind of umbrella is formed round the oral region.

There are three kinds of ambulacral appendages: the tube-feet and ambulacral papillae already mentioned, and the tentacles.

The **tentacles** contain a prolongation of the water-vascular system, usually of the radial canals, and are modified tube-feet. They vary in number from 10 to 30. The number is usually a multiple of 5, except in the Synaptidae, in which there are frequently 12, and is usually constant in the same species and even genus; but there are genera and even species in which the number is variable. In the Dendrochirotae with ten tentacles, the two ventral (adult) tentacles are usually smaller than the others (Fig. 177). They may be pinnate (Molpadiidae, Synaptidae), shield-shaped (Aspidochirotae), or dentritically branched

(Dendrochirotae). The tentacles and the part of the body carrying them are retractile.

The ambulacral feet terminate in a suctional disc which is provided with a perforated calcareous plate, while the ambulacatory papillae have pointed ends and the calcareous plates are reduced or absent. In the Elasipodidae calcareous plates are only exceptionally present even on the feet. No sharp line can be drawn between these two kinds of appendages; and it is often impossible to say whether we have to do with the one or the other. The ambulacral feet are essentially locomotory, while the papillae are respiratory and sensory. The distribution of these structures varies considerably even in the same genus. They may be arranged in radial rows, which may be single, double or multiple; or they may be scattered on radii and

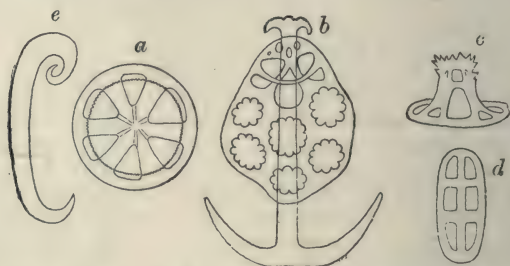


FIG. 178.—Calcareous bodies from the integument of Holothurians. *a* Calcareous wheels of *Chiridota*; *b* anchor with supporting plate of *Synapta*; *c* stool-like body; *d* plate of *Holothuria impatiens*; *e* hooks of *Chiridota*.

interradii alike. If there is a ventral sole, the three ventral radii are provided with feet and the dorsal radii with papillae, scattered or in rows. Sometimes the feet are absent from the median row of the sole (some Elasipodidae, Fig. 184), and in *Psolus* the dorsal surface is altogether without ambulacral appendages. In the Molpadiidae, Synaptidae and *Pelagothuria* both feet and papillae are absent, the tentacles being the only representative of ambulacral appendages.

There is a dermo-muscular body wall, which contains isolated calcareous spicules of various form (Fig. 178). Calcareous plates such as are found in other Echinoderms are feebly if at all developed and no representatives of the oral and apical systems of plates are found at any stage of life. The skin has a leathery consistency and may be covered with warts and ridges.

In *Myriotrochus* and many species of *Synapta* and *Chiridota* it is thin and transparent. The body wall consists of a single layer of non-ciliated epithelial cells which carry a cuticle, a thick cutis which consists of connective tissue and contains the calcareous bodies, a layer of circular muscles which is often interrupted in the radii, five radial bands of longitudinal muscles (Fig. 181), each of which may be double, and finally the layer of peritoneal epithelium lining the body cavity (Fig. 180). The cutis consists of a ground substance containing branched cells and fibres. The calcareous bodies of the cutis are minute in size and definite in shape*: they have the form of anchors, wheels, rods, perforated plates, stools, etc., and their shape and arrangement is of importance for the determination of species. They are found in the cutis of the tube-feet, ambulacral appendages, and tentacles, as well as in the body wall. In a few forms, e.g. *Psolus*, *Theelia*, the calcareous bodies of the dorsal side are large and plate-like and appear like protective scales. In the Dendrochirotae in which the anterior part of the body is invaginable, there are at the base of the invaginable part five calcareous plates—the **oral valves**, which cover over the aperture when the proboscis is withdrawn. Similar plates are sometimes found round the anus. Both oral and anal plates may be radial or interrarial in position.

Retractor muscles capable of retracting the anterior part of the body are found in the Dendrochirotae and some other forms (*Molpadia*, species of *Chiridota* and *Synapta*). They are muscular bands detached from the longitudinal muscles at about the middle of the body and inserted into the radial pieces of the calcareous ring (Fig. 179).

The **calcareous ring** consists of a circle of ten calcareous pieces—five radial and five interrarial—which surround the oesophagus (Fig. 181, 28). It is placed in the outer wall of the perioesophageal sinus (Fig. 179) on the oral side of the water-vascular ring but aboral of the nerve ring. The interrarial pieces of the ring may be wanting or there may be more than five interrarial pieces.

The **water-vascular system** consists of (1) a circular vessel

* In some Holothurians they appear to change their shape with advancing age, e.g. *Stichopus Japonicus*, *Ann. Zool. Japonenses*, 1, 1897, p. 35.

round the oesophagus placed aboral of the calcareous ring in the outer wall of the perioesophageal sinus (Fig. 179); (2) five

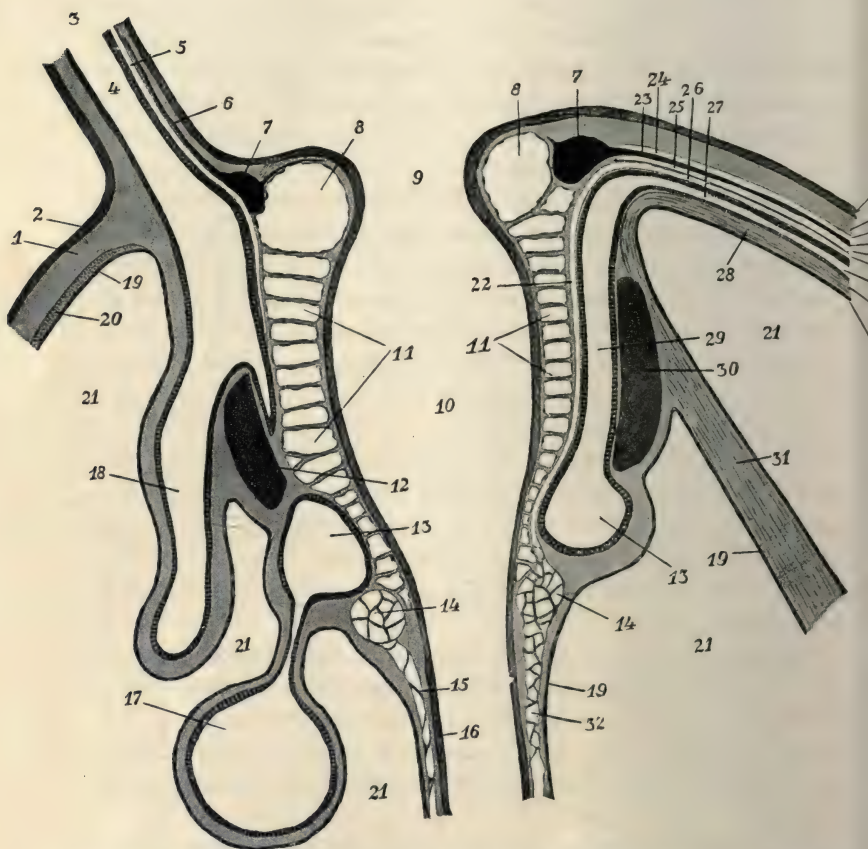


FIG. 179.—Diagram of a longitudinal section through the oral region of a Holothurian. The section passes through a radius on the right side, and through an interradius on the left (from Lang). 1 cutis, 2 ectoderm, 3 oral tentacle cut off, 4 canal of the oral tentacle, 5 blood-vessel of the oral tentacle, 6 tentacle nerve, 7 circumoral nerve, 8 oral portion of perioesophageal sinus, 9 mouth, 10 oesophagus, 11 perioesophageal sinus, 12 interradian piece of calcareous ring, 13 circumoral water-vascular vessel, 14 so-called blood-vascular ring, 15 ventral intestinal vessel of the so-called vascular system, 16 epithelium of alimentary canal, 17 polian vesicle, 18 ampulla of oral tentacle, 19 peritoneal epithelium, 20 circular muscles of body wall, 21 body-cavity, 22 and 26 radial vessel of vascular system, 23 radial trunk of superficial nervous system, 24 radial epineural canal, 25 radial perihæmal canal, 27, 29 radial canal of water-vascular system, 28 longitudinal muscles, 30 radial piece of calcareous ring, 31 retractor muscle, 32 dorsal intestinal vessel of vascular system.

radial vessels which travel oralwards to the anterior end of the body and then aboralwards in the radii of the body wall, just

outside the longitudinal muscular bands, to the apical pole, where they terminate blindly in the integument near the anus. There is no projecting terminal tentacle as in Asteroids and Echinoids. The radial canals are five in number; they are absent only in Synaptidae. The circular vessel has two appendages—the **polian vesicle** and the **stone-canal**. The polian vesicle (Fig. 181) is generally single and may be of large size; it is usually attached to the circular canal in the left adult-ventral interradius. Exceptionally, additional polian vesicles are present, generally in the adult-ventral region of the body. The stone-canal is usually single (always in Molpadiidae, Pelagothuridae and Elaspodidae), but in the Synaptidae, Aspidochirotae and Dendrochirotae it is occasionally multiple. When it is single it lies in the dorsal mesentery; when multiple, the primary canal alone is in the mesentery, and the accessory stone-canals which are very variable in number (2 to 160) project, mostly from the dorsal half of the ring-canal and on either side of the mesentery, freely into the body-cavity into which they open (see below). Occasionally the primary stone-canal is independent of the dorsal mesentery, and projects into the body cavity on the right-hand side (many Aspidochirotae). In a few species (*Thyone chilensis*, *Synapta beselii*) the stone-canal is branched, with a body-cavity opening at the end of each branch. The wall of the stone-canal is without muscles and usually contains calcareous deposits; the internal lining consists of a ciliated epithelium which on one side of the tube is composed of much more columnar cells than on the other. The termination of the stone-canal presents the most remarkable variations. In some it is attached to the body-wall and opens to the exterior in the dorsal middle line just in front of the generative opening either by a single pore (*Pelagothuria* and some Elaspodidae) or by more than one pore (2–50 or more, many Elaspodidae). In other cases (certain Elaspodidae and Molpadiidae) the stone-canal ends blindly in the body wall in the dorsal middle line, and opens, not to the exterior, but into the body-cavity by a number of pores which perforate its walls just before its blind end. In all other Holothurians it has lost its connexion to the body wall altogether, and opens into the body-cavity by a large number of pores placed upon its slightly swollen termination. It is remarkable that species of the same genus may differ in the

mode of termination of the stone-canal, as the following statement shows.

The stone-canal opens to the exterior by a single pore in *Pelagothuria* and in species of the following genera of Elasipodidae, *Scotoplanes*, *Kolga*, *Parelpidia*, *Elpidia*, *Peniagone*, *Benthodytes*; it opens to the exterior by more than one pore in the following genera of Elasipodidae, *Benthodytes*, *Psychropotes*, *Laetmogone*, *Iliodaemon*; it ends blindly in the body wall, opening into the body-cavity by several pores close to its blind end in species of the following genera of Elasipodidae *Irpa*, *Elpidia*, *Oneiropanta*, *Orphnurgus*, *Benthodytes*, and in the molpadian genera *Trochostoma* and *Ankyroderma*. In other Molpadiidae, in Synaptidae and Dendrochirotae it opens into the body-cavity as in the last named, but is without the blind part and the connexion to the skin; lastly in the Aspidochirotae the numerous pores lead from the body-cavity into a sac with which the stone-canal communicates by one or more openings. It is possible that this last arrangement gives the key to the explanation of these strange variations in the termination of the stone-canal. As has been fully described the stone-canal in other Echinoderms does not open directly to the exterior, but into a portion of the body-cavity, the axial sinus, which opens to the exterior by the water-pore or pores (madreporite) and is derived from the anterior body-cavity of the larva. In adult Holothurians there is apparently no trace of axial sinus or other derivate of the anterior body-cavity. But in the larvae, as Bury has shown, a representative of this cavity which has the appearance of being merely a small appendage of the stone-canal (p. 152, Fig. 108) is present. It is possible that the sac, into which the stone-canal of the Aspidochirotae opens and the small dilatation into which the body-cavity pores lead in some other forms, is the representative of the anterior body-cavity, which in other Holothurians is so much reduced that it is not even discernible as a dilatation on the stone-canal in the adult. On this view the pores of the so-called internal madreporite are secondary perforations in the septum which separates the much-reduced anterior body-cavity from the general body-cavity, the real water-pore being aborted; whereas in Holothurians with an external madreporite, the water-pore of the larva has persisted, but the anterior body-cavity into which it opens has become indistinguishable from the stone-canal.

The appendages of the radial canals consist of prolongations into the tube-feet and tentacles, and of some prolongations which ramify and end blindly in the body wall. The tentacular canals arise from the radial canals soon after their origin from the ring canal (Fig. 179). They are provided (except in Elasipodidae) with ampullae which project into the body-cavity. In the Synaptidae alone do they arise direct from the ring canal. The tube-feet prolongations arise alternately on each side of the radial canals. Ampullae are always present and either project into the body-cavity or are embedded in the body-wall between

the cutis and circular muscles (Elasipodidae). There is apparently no representative of the **axial organ**.

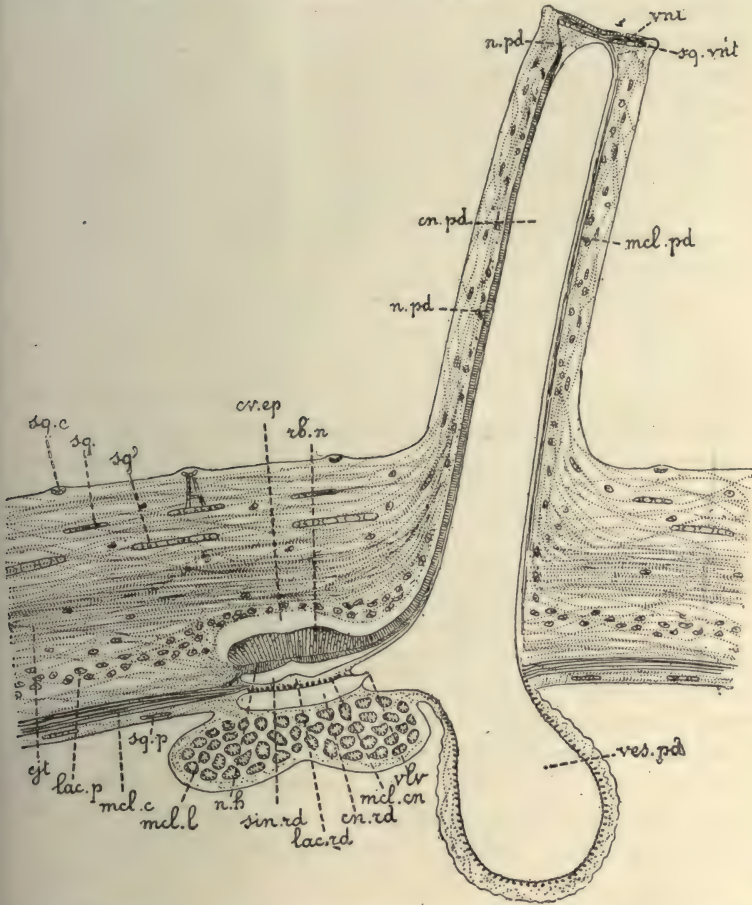


FIG. 180.—Diagram of a transverse section through the body-wall of a Holothurian in the region of a radius (after Delage and Hérouard). *cyt.* dermis; *cn.pd* cavity of tube-foot; *cn.rd* radial water-vascular vessel; *cv.ep* epineural cavity; *lac.p* lacuna in the skin; *lac.rd* radial vascular strand; *mcl.c* circular muscles; *mcl.cn* muscles of the radial water vessel; *mcl.l* longitudinal muscle of the radius; *mcl.pd* muscles of tube-foot; *nh* nerve cord of deep oral system; *n.pd* pedal nerve; *rb.n* radial nerve of ectoneural system; *sin.rd* radial periaermal canal; *sq, sq', sq.e, sq.p* skeletal pieces of the dermis; *sq.vnt* skeletal piece of the sucker of a foot; *ves.pd* ampulla; *vlv* valve; *vnt* sucker.

The **central nervous system** presents two parts only, the ectoneural ventral system and the deep oral system. There is apparently no apical system.

The ventral system consists of a circumoral ring and five

radial prolongations, and lies as in all other classes in the ectoderm, but the ectoderm containing it is separated from the surface and forms the lining of an epineural canal (Fig. 180, *cv.ep.*) as in Ophiuroids and Echinoids. The circumoral part (Fig. 179, 7) lies immediately round the mouth in the inner wall of the circumoral part of the epineural canal (not shown in the figure), and the radial nerves extend along the whole length of the radius almost as far as the anus. This system gives off branches to the tentacles, tube-feet, and skin, and, from its circumoral part, to the gut. In the skin there is a subepithelial nervous plexus in the dermis.

The deep oral system is obscurely double (Fig. 180, *nh*). It lies in the outer wall of the radial periaermal canal, to the epithelium of which it has the same relation as has the ectoneural system to the ectoderm. It is so closely applied to the radial cords of the ectoneural system, that it was not till the publication of Hérourard's important work on the group that the two were distinguished. It extends along the whole length of the radius and is without any circumoral part.

Sense organs. Integumentary sense organs are of course present, but there does not appear to be an organ for the perception of light. Otocysts are present in the Synaptidae and Elasipodidae. In the Synaptidae there are five pairs of them placed on the radial nerves at the point where these pass beyond the calcareous ring. In the Elasipodidae they are more numerous (from 14 to more than 100) and they occur along the course of some or all of the radial nerve trunks. They have numerous small otoliths and a ciliated lining. In the Synaptidae the otoliths are vesicular cells with a fluid contents and collapse and disappear when the animal is placed in spirit.

The alimentary canal. The mouth, though really terminal, may in consequence of the curvature of the axis appear to be on the dorsal (*Psolus*, *Theelia*, *Psolidium*, *Colochirus*) or ventral (many Aspidochirotae and Elasipodidae) surface (see p. 267). It is without any armature of teeth or papillae and is placed in the midst of the tentacular circlet. It leads into the oesophagus which a little behind the water-vascular ring is continued, often without any marked line of demarcation, into the stomach. The stomach is short and tubular and is continued, again often

without any marked line of separation, into the intestine. The intestine after a short course backwards turns forwards and extends to near the front end of the body (Fig. 181), where it again bends backwards to pass to the rectum or cloaca, which opens by the anus at the hind end of the body. The alimentary canal is connected to the body wall along its whole length by a mesentery which is mainly derived from the dorsal mesentery of the larva. It is therefore larval-dorsal, but in the adult its attachment is different in the different parts of the tube. The first reach of the alimentary canal, consisting of oesophagus, stomach and

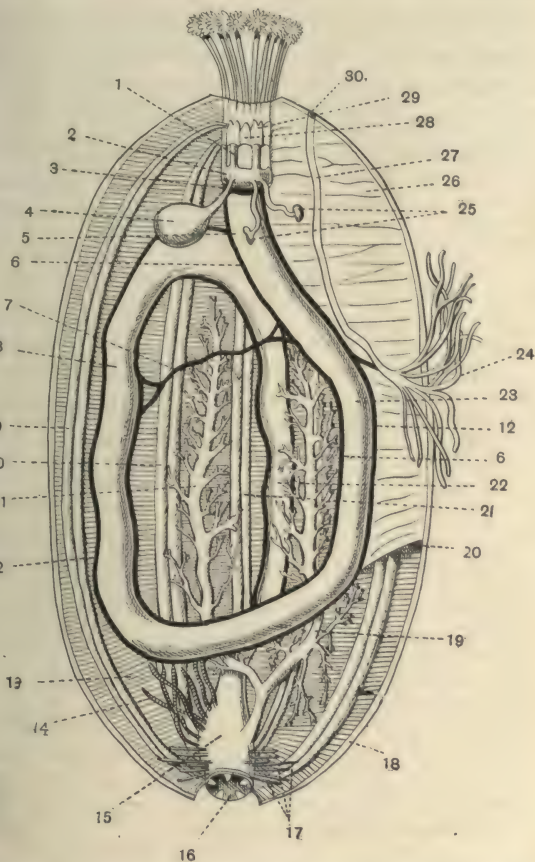


FIG. 181.—One of the *Aspidochirotes* opened and viewed from the left side, diagrammatic (from Leuckart's Wandtafeln). The body wall has been cut through just to the left of the dorsal middle line. The mouth is at the upper end and surrounded by tentacles. The tentacular ampullae are not represented. 1 radial vessel leaving the water-vascular ring 2; 3 blood-vascular ring; 4 polian vesicle; 5 oesophagus; 6 ventral blood-vessel of the first and second part of the intestine; 7 vessel connecting the ventral blood-vessel of the first and second part of the intestine; 8 second part of the intestine; 9, 10 radial longitudinal muscle; 11 left respiratory tree; 12 dorsal blood-vessel of intestine; 13 circular muscles of body-wall; 14 cuvierian organs; 15 cloaca; 16 anus; 17 radial muscles of cloaca; 18 cut edge of body-wall; 19 right respiratory tree; 20 posterior edge of the dorsal mesentery; 21 median ventral longitudinal muscles; 22 third part of intestine; 23 first part of intestine; 24 gonad; 25 so-called internal madreporites of two stone-canals; 26 dorsal mesentery; 27 genital duct; 28 inter-radial, 29 radial piece of the calcareous ring; 30 genital opening.

anterior part of intestine is attached by a dorso median (adult) mesentery (Fig. 181, 26) to the body wall in the dorsal inter-radius (Fig. 182, M_1). At the first bend the mesentery passes across the left dorsal radius to the left dorsal interradius, where it is attached all along the second or forward reach of the intestine (M_2). At the second bend the mesentery passes across the intervening radii and interradii into the right ventral interradius, where it is attached all along the third backwardly directed reach of the intestine (M_3). In *Synapta* the alimentary canal is straight, but as is

shown by the attachment of the mesentery it has the same spiral course round the body wall as that just described. The anus, which is typically terminal, may, like the mouth, be apparently shifted on to the dorsal or ventral surface.

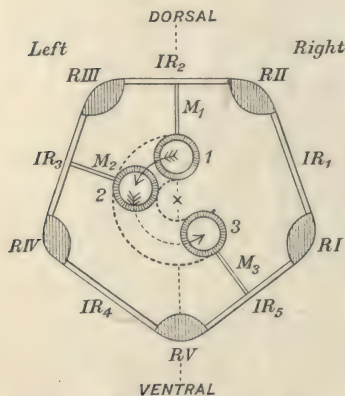


FIG. 182.—Diagrammatic transverse section through a Holothurian seen from the aboral pole, to show the course of the gut, the attachment of the mesentery and the enumeration of the radii adopted in the text. The vertical dotted line gives the position of the median plane, and the x the position of the transversely cut vertical axis. 1, 2, 3 represent the three stretches of the alimentary canal, and M_1 , M_2 , M_3 the mesenteries attaching them. RI–RV mark the radii numbered, and IR₁–IR₅ the interradii. IR₂ is the dorsal interradius of the bivium, which contains the water-pore and generative opening.

The wall of the gut consists of (1) an internal epithelium which has a cuticle and may be ciliated, (2) a layer of connective tissue containing blood spaces, (3) a muscular layer consisting of longitudinal and circular fibres, (4) an outer connective tissue layer, and (5) the peritoneal epithelium.

The respiratory trees (Fig. 181) are two hollow much-branched structures placed right and left in the body cavity and opening together or by separate openings into the cloaca. The ultimate branches of the organ end in ampulla-like dilatations which may also be found along the course of the branches themselves.

The walls consist of (1) an inner, probably ciliated, epithelium often in more than one layer; projections into the cavity, caused by cells containing yellow pigment granules, are present; (2) a connective tissue layer, (3) a muscular layer, (4) an outer connective tissue layer, and (5) a layer of peritoneal epithelium. The respiratory trees do not communicate with the body-cavity, and they are absent in the Synaptidae and Elaspodidae, but in the latter group there is a forwardly directed caecum

which opens into the cloaca and may represent them. The number of respiratory trees is never more than two, the apparent exceptions to this rule being caused by some of the branches acquiring a great distinctness. The function of these organs is probably respiratory, the cloaca apparently having the power of sucking up water and of driving it into them, and then of expelling it. Rhythmical inspiratory and expiratory movements of the cloaca and to a certain extent of the body appear to effect this. They may also be partly excretory, for the expelled water besides carrying faeces also contain various kinds of cell débris including cells with brown granulations, which probably originate on the walls of the "trees."

The **cuvierian organs** (Fig. 181, 14) are tubular organs which open into the terminal parts of the respiratory trees. The number varies in different species, but as many as 100 have been counted in one individual. They are usually unbranched, but they may be branched or even racemose. They are found mainly in the Aspidochirotae, especially in the genera *Holothuria* and *Mülleria*, but they appear to be entirely absent in *Labiododemas*, *Pseudostichopus*, *Paelopatides*, and *Stichopus* (*St. paradoxus* excepted). They are unknown in Synaptidae and Elasipodidae and are only exceptionally found in other families (e.g. *Molpadia chilensis*, *Cucumaria frondosa* and *nigricans*). They are probably to be regarded as modified branches of the respiratory trees. The unbranched tubes are lined with an epithelium, outside which is a layer of connective tissue. This is followed by an internal circular and an external longitudinal muscular layer, the internal circular layer consisting of a closely wound spiral fibre. Then comes an outer connective tissue layer and finally the peritoneal epithelium, which in the case of the glandular cuvierian organs appears to be peculiarly modified and to secrete a sticky substance. In some Holothurians (the so-called cotton-spinners) the cuvierian organs can be ejected from the cloaca when the animal is irritated and used as organs of defence. This phenomenon has been studied in *Holothuria nigra* (*forskali*),* and in *H. poli*,† and in other forms.‡ When the skin is irritated a small number of these organs make their way, blind end forwards, through a rent which is formed in the dorsal wall of the cloaca. On emerging from the anus they rapidly undergo elongation to twenty or thirty times their original length, darting about in all directions and becoming attenuated in the process. They stick by their viscid surface to everything they touch (except the surface of the animal itself). If the Holothurian now moves away they become detached from its body by rupture. The cause of the active elongation and movement of the tubes is not clearly known. It is not apparently due to injection of fluid from the respiratory trees because it can take place if the tubes are detached from the animal. It would appear to be caused by some process taking place in the wall of the tube itself. When first ejected each tube is thicker at the free end than at the base. The elongation appears to take place at the expense of this "head" which diminishes in length during the process. The elongation is said to begin while the organs are still in the body-cavity and can be brought about by direct irritation of the tubes themselves as well as of the skin. The tubes after elongation cannot be shortened and must therefore be cast off, new tubes being presumably

* Minchin, *Ann. and Mag. Nat. Hist.* (6), 10, 1892, p. 273.

† Barthels, *Verh. Nat. Ver. Bonn*, 53, 1896, p. 76.

‡ Semper, *op. cit.* Peach, *Ann. and Mag. Nat. Hist.*, 15, 1845, p. 171.

formed from the respiratory trees. The branched cuvierian organs have not got the viscid wall and their function is not understood.

The **coelom** presents the usual main divisions, viz. (1) the ambulacral system (2) the perivisceral cavity, and (3) the perihæmal spaces. The ambulacral system has already been described.

The **perivisceral cavity** is spacious and is traversed by the dorsal (larval) mesentery (see p. 257), and by muscular and connective strands. It is lined by a ciliated epithelium and contains a corpusculated fluid. It has so far as is known no communication with the exterior, but in many Holothurians it communicates with the water-vascular system through the so-called inner madreporite.

There is a special section of the body-cavity round the oesophagus, called the perioesophageal sinus (Fig. 179, 8, 11). This is separated from the rest of the body-cavity by a membrane, which however is in most cases perforated by apertures putting it in communication with the general body-cavity, and it is traversed by strands of tissue passing from the wall of the oesophagus to this outer wall of the sinus, except just round the mouth opening where it is free from trabeculae and constitutes the peribuccal sinus. In the *Elasipodidae* the outer membrane is complete and the perioesophageal sinus is completely shut off from the rest of the body-cavity.

In the *Synaptidae* there is a number of **funnel-shaped ciliated organs** attached by a stalk to the mesentery and body wall. The cavity of these organs, which is freely open to the body cavity, is lined by a ciliated epithelium and ends blindly in the stalk. The stalk may be branched and carry many ciliated funnels.

The **perihæmal spaces**, which are almost certainly parts of the coelom, are lined by a flat epithelium and contain a fluid similar to that of the body-cavity. They consist of five radial canals (Fig. 180, *Sin.rd*) placed just internal to the radial nerves, between these and the radial blood-vessels. A circumoral perihæmal canal has been described in some cases (*Synapta*, *Cucumaria*, etc.).

In the *Synaptidae* the perihæmal canals do not extend very far from the oral region, and the circumoral perihæmal space is separated by a septum from the radial perihæmal spaces. The perihæmal spaces appear not to communicate with the perivisceral cavity.

The **vascular system**. Immediately aborad (Fig. 179, 14) of the water-vascular ring is the circumoral vessel of the so-called vascular system. This sends off to each radius a vessel which extends to the aboral end of the body just external to the water-vascular canal (Fig. 180, *lac.rd*). It is also connected

with two intestinal vessels, one of which lies on the mesenterial side of the intestine close to the insertion of the mesentery, and the other on the opposite, non-mesenterial side (Fig. 181).

In many Holothurians (most Aspidochirotae, some Dendrochirotae and Molpadiidae) the dorsal gut vessel (mesenterial) becomes detached in part of its course from the intestinal wall (Fig. 183), but remains connected with the blood lacunae in the intestinal wall by a plexus of vessels passing across the body-cavity. This plexus is the *rete mirabile*. The dorsal vessel and rete mirabile lie on the same side of the mesentery. It often forms a kind of web which loosely invests the terminal branches of the left respiratory tree. These vessels are connected with lacunae in the walls of the neighbouring organs. The intestinal vessels are connected with lacunae in the inner connective tissue coat of the alimentary canal; the circular vessel supplies the tentacular canals, the stone canal and the polian vesicle, the oesophagus and often the gonad; the radial vessels give off branches to the tube-feet and papillae; and lastly the lacunae in the walls of the gonad may be supplied from the dorsal (mesenterial) intestinal vessel, or from the circular vessel.

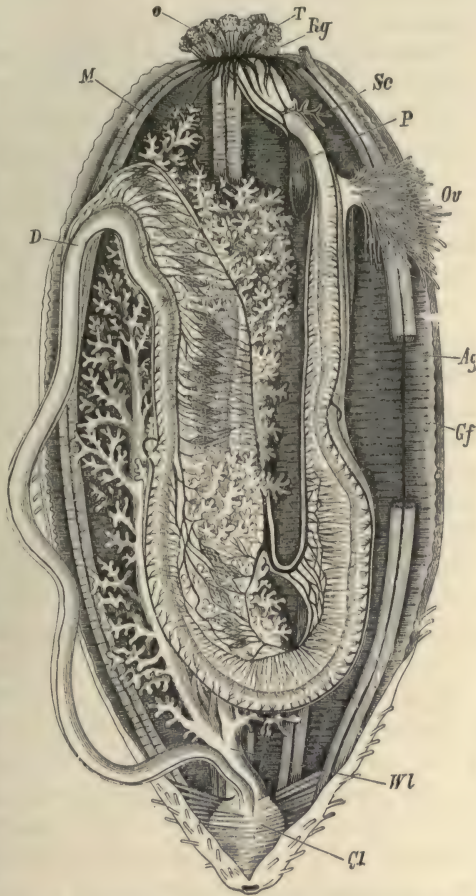


FIG. 183.—*Holothuria tubulosa* opened longitudinally (from Claus, after M. Edwards). O mouth in the midst of the tentacles T; D alimentary canal; Sc stone-canal; P polian vesicle; Rg circular vessel of the water-vascular system; Ov ovary; Ag radial water-vascular canal; M longitudinal muscles; Gf intestinal vessel; Cl cloaca; Wl respiratory trees.

The vascular system is composed of tissue similar to that found in Asteroids and Echinoids, but containing better defined

channels. The vascular trunks though called vessels are nothing more than a system of communicating spaces or bundles of anastomosing tubes. They are without any epithelial lining, and contain a coagulable fluid.

Reproductive organs. The Holothurians are for the most part dioecious, but a few of the Synaptidae and Molpadiidae are hermaphrodite (ova and spermatozoa arising in the same tubes). The gonad is single and lies in the adult-dorsal interradius (Fig. 181). It consists of a tuft of branched tubes projecting into the body-cavity, on both sides of the mesentery (on the left side only in *Holothuria*, *Mülleria*, *Labidodemas* and some *Elasipodidae*). The genital duct lies in the dorsal mesentery and opens to the exterior in the middle, adult-dorsal line in the anterior region of the body. In the *Dendrochirotae* it is between two of the tentacles or even within the tentacular circle; in the *Molpadiidae* and *Synaptidae* it is immediately behind the tentacular circle; it is furthest removed from the tentacles in the *Elasipodidae* (in *Psychropotes longicauda* it lies in the posterior half of the body). The genital duct is always single, but in some *Elasipodidae* it divides so as to open by several apertures (in some species the number varies in different individuals). The genital opening may be at the end of a small papilla. The genital rachis, if present, is represented by a cord near the genital duct (p. 132).

As a rule there are no external sexual differences, but the sexes can sometimes be distinguished by inspection of the generative organs. In a few species the male alone possesses a genital papilla (*Thyone aurantiaca*, *Cucumaria laevigata*, etc.). In the connective tissue layer of the wall of the gonad, which lies next the inner epithelium, there is an extensive development of the lacunar spaces of the blood-system.

They are all marine, and with the exception of one pelagic form (*Pelagothuria*) they live on the sea bottom, usually attached to external objects by their tube-feet. Most of them are able to crawl by means of their tube-feet, though many of them move but little. Many of those which have been observed are said to be more active during night than in the day time, but no visual organs are known. They are found in all seas and at all depths, many being littoral and a considerable number abyssal. The *Elasipodidae* are almost entirely deep-sea forms. The *Synap-*

tidae and Molpadiidae, which are without tube-feet, are burrowers.

The skin in some forms secretes a slimy substance, which in some cases appears to be used for entangling small food organisms. In *Pseudostichopus mollis* and *occultatus* the body is covered with the shells of Foraminifera.

They feed on the smaller marine animals, which in the *Dendrochirotae* are collected and carried to the mouth by the large tentacles. These tentacles are used for this purpose one at a time. The two small tentacles are applied alternately over the mouth so as to close it or wipe it in the intervals between the introduction of food by the large tentacles. The *Aspidochirotae* fill their intestine with sand, which they eject from the anus together with the current of water from the respiratory trees. It is worthy of notice that many Holothurians (especially the *Aspidochirotae*) have the power when irritated of ejecting through the anal opening the alimentary canal (and its appendages) which breaks off behind the vascular ring and in the region of the cloaca. They are able to regenerate the parts so lost, sometimes with considerable rapidity. In some cases this ejection includes the gonad, the calcareous ring and tentacles. The ejected organs seem to be distasteful to other animals, and if taken up are soon rejected. This ejection of the viscera is said not to occur in *Cucumaria* or in the Elaspodidae. In the *Synaptidae* the body, when irritated, breaks into several pieces by violent muscular contractions of the body wall. The anterior of the pieces so produced is able to regenerate the rest of the body. Asexual reproduction by division is said to take place in *Cucumaria planci*, etc.*

Of parasites found in Holothurians may be mentioned *Entovalva mirabilis*, a bivalve mollusc living in the pharynx of species of *Synapta* (vol. i. p. 349), the Gastropods, *Eulima* and *Stylifer* in the gut and on the skin of various *Aspidochirotae*, *Entoconcha* in the body cavity (*Synapta* and *Holothuria*), and *Entocolax* from the inner side of the body wall of *Myriotrochus rinkii* (vol. i. p. 403). Finally the remarkable commensal *Fierasfer*, a Teleostean fish, lives in the right respiratory tree of *Aspidochirotae* (vol. 2, p. 227).

They vary in length from 5 to 60 cm. (*Cucumaria frondosa*

* Chadwick, *Proc. and Trans. Liverpool Biol. Soc.*, 5, 1891, p. 81.

Gunn.) but the Synaptidae may attain a length of from one to two metres.

Certain species of the genera *Holothuria* and *Stichopus* form an important article of commerce in the East, being used by the Chinese for the preparation of a highly esteemed soup, etc. They are known as Trepang and Bêche de mer.

They are not suitable for preservation as fossils, but remains of their spicules have been described from the Carboniferous, the Jurassic, the Cretaceous and the Eocene formations (*Synapta*, *Chiridota*, *Myriotrochus*).

The development is sometimes direct, but more usually there appears to be a bilateral larva called *Auricularia* which arrives at the adult condition by passing through a barrel-shaped pupa stage. In *Phyllophorus urna* Gr., *Synapta vivipara* Oerst., and *Chiridota rotifera* Pourt., the eggs make their way into the body-cavity, where they are fertilized and undergo their development. This phenomenon has been examined in the case of *Synapta vivipara* by Clark * who states that the eggs escape into the body-cavity through the walls of the genital tubes and that the spermatozoa make their way into the sea through the genital duct and then enter the cloaca, through the walls of which, either by means of fine pores or by actual penetration, they enter the body-cavity and fertilize the ova. The young escape from the body-cavity by rupture of the body wall or of the intestinal wall. In some forms the eggs are received into two ventrally placed pouches (*Cucumaria minuta* Fabr. (*glacialis*) and *laevigata* Verr.), in others into a dorsal pouch (*Psolus ephippifer* W. Thoms.). In some they are attached to the dorsal integument (*Cucumaria crocea* Less.), and in *Cucumaria planci* the eggs are retained for some time amongst the tentacles. As a rule, however, both ova and spermatozoa are spawned direct into the sea, and the young are developed independently of the mother. Direct development within the egg membranes occurs in *Cucumaria kirchbergii* (*Psolinus brevis*, Kowalevsky, *op. cit.*), and possibly in those forms which develop in brood-pouches. In *Phyllophorus urna* (Kowalevsky, *op. cit.*) a ciliated larva is formed, which swims about in the body-cavity and possesses 5 tentacles and 2 tube-feet when it leaves the parent. In *Cucumaria planci*

* *Mem. Boston Soc. Nat. Hist.*, 5, 1898, p. 53.

the embryo passes at once into the stage of the barrel-shaped larva. It is said that the eggs of *Cucumaria kirchbergii* are already fertilized when they leave the body of the mother.

With regard to **affinities** we think that there can be no doubt that the Holothurians must be placed apart from the three preceding classes of Echinodermata. They differ from these in a number of anatomical features which we cannot but regard as of fundamental importance. For instance, in the embryo, the inconspicuousness of the anterior coelom; in the adult, the absence of radial repetition of the gonad, and the absence of the axial sinus and axial organ, and the absence at all times of life of the plates of the apical system. The absence of pentamerous structure in the alimentary canal cannot be regarded as so important, for the same negative feature is characteristic of Echinoidea. Neither can the fact that the blastopore gives rise to the permanent anus, or that the larval mouth and anus both persist into the adult, be regarded as of fundamental importance having regard to the varied behaviour of these structures in other animals. But although it is undoubted that the Holothurians must be placed apart from Asteroids and Echinoids, still it cannot be said that they approximate to the Crinoids, for those very features which separate them from the first, separate them also from the last. The anterior coelom, the radial repetition of the gonads, the axial organ and the apical plates are all present and well-developed in Crinoids, though the anterior coelom disappears in the adult. Indeed we may go further and say that Holothurians stand further from Asteroids and Echinoids than do the Crinoids, for whereas Asteroids and Echinoids agree with Crinoids in the above-named anatomical characters, the only point of importance which they have in common with Holothurians and which is not also found in Crinoids is the form of the free larva. For these reasons we hold that out of the primeval matrix of the Echinodermata three main groups have emerged and persisted to the present day; these are (1) the Asteroids, Ophiuroids and Echinoids, (2) the Holothuroids and (3) the Crinoids.

Order 1. ACTINOPODA.

All external appendages of the water-vascular system arise from the radial canals, and have the form of tentacles round the mouth and of ambulacral feet and papillae on the body. Tentacles are always present, but feet and papillae may be absent.

Sub-order 1. **ASPIDOCHIROTAE**. With 18-30 shield shaped tentacles (except *Molpadiidae*). Ampullae of the tentacular canals, respiratory trees, and cuvierian organs present or absent. Without retractor muscles of the pharynx (present in *Molpadia*).

Fam. 1. **Holothuriidae**. Body cylindroidal. Solelike ventral surface usually but slightly developed. The ampullae of the tentacular canals are well developed and project into the coelom. The calcareous ring is formed of 5 radial and 5 interradial pieces. Otolithic vesicles are absent. Stone-canals often numerous, opening into the body-cavity. Longitudinal muscles usually divided; retractor muscles absent. Respiratory trees well developed, the left being usually covered by the plexus of the intes-

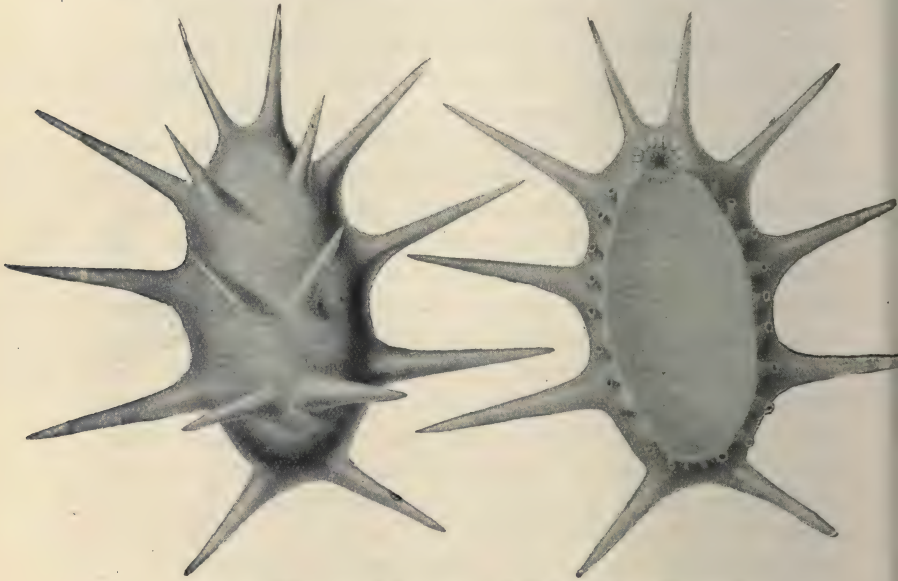


FIG. 184.—Dorsal and ventral view of *Deima atlanticum* (after Hérouard).

tinal vascular system. Cuvierian organs present. Mainly in the indo-pacific region and littoral. *Mülleria* Jäger, anus with calcareous teeth; the other genera are without these. *Holothuria* L., trepang, ambulacral appendages over whole body, not in rows, cosmopolitan; *Labiododemas* Selenka, with feet only which are confined to the radii; *Pseudostichopus* Théel; *Stichopus* Brandt, trepang, with flat ventral surface on which there are usually three rows of feet.

British genus, *Holothuria* with species :

With pedicels only, *H. intestinalis* A. and R.

„ pedicels and papillae, *H. tremula* Gunn.

„ pedicels almost entirely ventral, *H. nigra* auct.

„ two rows of pedicels on either side of body, *H. aspera* Bell.

Fam. 2. **Synallactidae**. Body rarely cylindrical, generally flattened and with a ventral sole. Tentacular canals without ampullae. The stone-

canal is single and usually joins the body-wall. Neither of the respiratory trees are connected with the vascular network of the intestine. Abyssal forms. *Synallactes* Ludw. *Meseres* Ludw. *Bathyplores* Oest. *Bathyharpystikes* Sluiter. *Benthothuria* R. Perrier. *Pseudostichopus* Théel. *Mesothuria* Ludw. *Paeopatides* Théel. *Zygothuria* R. Per.

Fam. 3. **Elasipodidae**. Mouth more or less ventral. Ventral surface usually flattened to a solelike surface with three rows of feet (trivium). With 10, 15 or 20 more or less shield-shaped tentacles, without ampullae. Calcareous ring of 5 radial pieces or of 5 radial and 5 inter-radial complete or incomplete pieces. Otocysts generally present on the radial nerves. Stone-canal attached to the skin and often opening to exterior. Longitudinal muscles simple, retractors absent. Respiratory trees absent or vestigial. Cuvierian organs absent. For the most part abyssal.

Sub-fam. 1. **Deimatinae**. Body generally elongated. Calcareous ring well developed. Ventral surface flattened, the unpaired radius being without or with reduced feet. Tube-feet serially arranged. *Deima* Théel (Fig. 184). *Oneirophanta*, *Orphnurgus*, *Laetmogone*, *Ilodaemon*, and *Pannychia* Théel. *Scotodeima*, *Laetmophasma*, and *Capheira* Ludwig. *Benthogone* Koehler.

Sub-fam. 2. **Elpidiinae**. Usually with 10 tentacles. Ventral surface flattened, the unpaired radius being always without feet. The dorsal ambulatory appendages much reduced in number and the latero-ventral feet are frequently confined to the hinder part of their radii. The calcareous ring is without the interradiial pieces. *Peniagone* Théel. *Elpidia* and *Parelpidia* Théel. *Irpa* and *Kolga* Dan. and Kor. *Scotoplanes*, *Achlyonice*, *Scotoannassa*, and *Enypniastes* Théel. *Rhipidothuria* Hérouard.

Sub-fam. 3. **Psychropotinae**. With 10 to 20 tentacles. Unpaired ventral ambulacrum with two rows of feet, rarely naked. The dorsal ambulacra with papillae all along their length or only in front. A large appendage sometimes projects from the hinder part of the dorsal surface. Calcareous ring with 5 separate calcareous pieces. *Benthodytes*, *Euphronides*, *Psychropotes* (Fig. 185), *Psychrotrepes* Théel.

Fam. 4. **Pelagothuriidae**. Pelagic forms of medusa-like appearance.

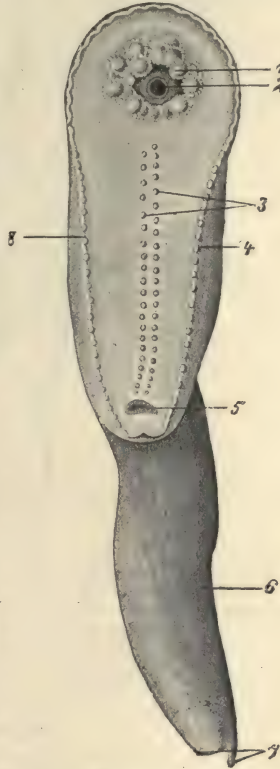


FIG. 185.—*Psychropotes longicauda* (from Lang, after Théel). 1 oral tentacles, 2 mouth, 3, 4, 8, ambulacral appendages of the trivium (adult-ventral); 5 anus; 6 dorsal appendage with its two posterior processes (7).

Tube-feet and ambulacral papillae absent. Mouth and anus terminal. Body cylindrical; round the tentacular circlet it widens out into a thin disc, the edge of which is produced into long rays; 13 to 16 tentacles; the tentacular canals arise from the well-developed radial canals, and they each give off at their base a canal (? ampulla) into the disc. Calcareous ring absent. The stone-canal opens on the surface of the body. Longi-



FIG. 186.—*Pelagothuria natatrix* (from Lang, after Ludwig), seen from the aboral pole.

tudinal muscles simple; retractors absent. Transverse muscles interrupted in the radii. Respiratory trees, ciliated cups and Cuvierian organs absent. Genital organs right and left of the dorsal mesentery. They swim on the surface of the sea by means of their disc. *Pelagothuria* Ludwig.

Fam. 5. **Molpadiidae.** Burrowers. Feet and ambulacral papillae absent. Mouth terminal. Hinder end of body often reduced to a tail-like appendage.

Tentacles small, usually 15 in number, cylindrical or provided with some small branches near the end; tentacular ampullae present, projecting into body-cavity. Calcareous ring of 5 radial and 5 interradial pieces. Stone-canal always single, often fastened to the body-wall. Otolithic vesicles absent. Longitudinal muscles divided, retractors well developed in *Molpadia* only. Respiratory trees present. Cuvierian organs only in one species. Principally on mud or clay. *Molpadia* Cuv., *Eupyrus* Lütken, *Haplodactyla* Grube, *Caudina* Stimp., *Trochostoma* D. and K., *Ankyroderma* D. and K., anchor shaped spicules in this genus.

Sub-order 2. **DENDROCHIROTAE**, with branched tentacles and retractor muscles of the pharynx. Tentacular ampullae (not projecting), and respiratory trees always present.

Fam. **Cucumariidae.** With feet, rarely with ambulacral papillae. Mouth usually dorsal or terminal. Anus often dorsal. Body cylindrical or pentagonal or with a ventral sole. With 10–30 branched tentacles often unequal in size, the two ventral being generally smaller than the rest (Fig. 177); tentacular ampullae not distinct. Calcareous ring of 5 radial and 5 interradial pieces. Otolithic vesicles absent. Stone-canal never opening to exterior. Retractor muscles well developed. Respiratory trees always, Cuvierian organs only occasionally present.

Cucumaria Blainville (Fig. 177), 10 tentacles, feet in rows on the radii; *Thyone* Semper, feet over whole body; *Orcula* Troschel, *Phyllophorus* Grube, with an inner row of smaller tentacles; *Pseudocucumis* Ludwig;

Actinocucumis Ludwig; *Colochirus* Troschel, feet in rows on ventral surface; *Psolidium* Ludwig; *Théelia* Ludwig; *Psolus* Oken with 10 tentacles, a ventral creeping sole, dorsal surface arched without ambulacral appendages, often with calcareous scales; principally arctic and antarctic. *Rhopalodina* J. E. Gray, mouth and anus close together at the end of stalk-like process, the dorsal interradius much shortened; on account of the peculiar course of the radial canals there appear to be ten radii. On the Congo coast. *Ypsilothuria* E. Per. (*Sphaerothuria* Ludw.).

British genera and species :

Cucumaria :

A. Tube-feet confined to ambulacra.

I. Tube-feet non retractile.

Skin smooth *C. hyndmani* Forbes.

Skin stiff *C. lactea* F and G.

II. Tube-feet retractile.

a Skin smooth.

Attenuated at either end *C. pentactes* Mont.

Body sac-like or elongated *C. planci* Gmel.

b Skin rough *C. hispida* Barr.

B. Tube-feet scattered *C. frondosa* Gunn.

Thyone : Body not curved on itself, *T. fusus* O. F. M. Body curved on itself, *T. raphanus* D. and K.

Psolus : Tube-feet in 3 complete rows, *P. phantapus* Struss., tube-feet of median row few or none, *P. fabricii* D. and K.

Phyllophorus : *P. pellucidus* D. and K., *P. drummondi* Thomp.

Order 2. PARACTINOPODA.

The oral tentacles arise from the circumoral vessel. Tube-feet and ambulacral papillae, respiratory trees and cuvierian organs are not present.

Fam. **Synaptidae**. Radial canals absent in the adult. Mouth terminal. Body cylindrical, worm-like. 10-27 (often 12) feathered tentacles; tentacular ampullae only indicated. Calcareous ring often with more than 5 interradii pieces. Anchor-shaped spicules are present in *Synapta* and its allies. Wheel-shaped spicules in most other genera. Stone-canal sometimes multiple. Otocysts on the origin of the radial nerves. Longitudinal muscles usually undivided; retractor muscles sometimes present. Respiratory trees absent. Ciliated organs on the wall of the body-cavity present, cuvierian organs absent. Generative organs often hermaphrodite. *Synapta* Eschscholtz, in sand and mud; *Euapta*, *Chondroclaea*, and *Labioplax* Oestergren; *Anapta* Semper; *Chiridota* Eschsch.; *Trochodota* Ludwig; *Trochoderma* Théel; *Myriotrocha* Steenstrup; *Acanthotrochus* D. and K. British species: *Synapta inhaerens* O. F. Müll.; *S. buski* MacInt., rare, *S. digitata* Montagu, British and French coasts, etc.

Class CRINOIDEA *

Brachiote Echinoderms attached during the whole or part of life by the aboral apex of the body. The arms are usually provided with pinnules and branched, the tube-feet are tentacle-like and without ampullae, the water-pore is always multiple, and the anus is interradially placed on the oral surface.

All living Crinoids are, so far as is known, attached, either in the young state only (Comatulids, *Thaumatoocrinus*) or throughout life, by a jointed stalk proceeding from the apical point of the body. The body consists of a calyx or disc, and of radial branched prolongations of the disc—the arms. The branches of the arms may be all alike, or some of them, known as *pinnules*, may differ in structure from the others. In the natural position of the animal the abactinal (dorsal of adult) surface is turned towards the substratum, to which indeed it is, as already stated, generally fixed by a stalk, while the actinal (ventral of adult) surface is directed upwards.

The actinal surface of the calyx is called the **calyx-cover** (*tegmen calycis*) and bears, usually † in its centre, the mouth, from which radiate towards the periphery on the calyx-cover the ambulacral grooves (food grooves). The portions of the

* J. S. Miller, *A Natural History of the Crinoidea or Lily-shaped Animals*, Bristol, 1821. J. V. Thompson, "Sur le *Pentacrinus Europaeus*, l'état de jeunesse du genre de *Comatula*," L'Institut, 1835. Id., "Memoir on the Starfish of the genus *Comatula*," *Edinburgh New Phil. Journ.*, 20, 1836. J. Müller, "Ueu d. Bau. v. *Pentacrinus caput medusae*," *Abhand. d. Berlin Akad.*, 1841. Id., "Ueb. d. Gattung *Comatula* u. ihre Arten," *ibid.*, 1847. W. B. Carpenter, Researches on the Structure, Physiology and Development of *Antedon rosaceus*, *Phil. Trans.*, 156. H. Ludwig, Crinoiden, *Z.f.w.Z.*, 1877, 28, p. 257; and 29, p. 47. P. H. Carpenter, "Report on the Crinoidea," *Challenger Reports*, I, "The stalked Crinoids," 1884, and II, "The Comatulæ," 1888. M. Neumayr, Die Stämme des Thierreiches, I, 1889. C. Wachsmuth and F. Springer, "Revision of the Palaeocrinoidea," *Proc. Acad. Nat. Sci. Philadelphia*, 1879, 1881, 1885. Id., "Discovery of the ventral Structure of *Taxocrinus* and *Haplocrinus*, etc." *Ibid.*, 1889. Id., "The perisomic plates of Crinoids," *Ibid.* 1890. Id., North American *Camerata*, *Mem. Mus. Harvard*, 20 and 21, 1897. E. Perrier, "Memoire sur l'Organisation et le developpement de la Comatule de la Mediterranée," *Nouv. Archives Mus. Hist. Nat. Paris*, 1886-92. H. Bury, "The early stages in the development of *Antedon rosacea*," *Phil. Trans.* 179, 1888. O. Seeliger, "Studien zur Entwick. der Crinoiden," *Zool. Jahrb., Abth. f. Anat.* 6, 1892. H. Ludwig, *loc. cit.* F. A. Bather, "British fossil Crinoids," a series of papers in *Ann. and Mag. Nat. Hist.* (6), 5, 1890. Id., The Crinoidea of Gotland, Pt. 1. *Kongl. Svenska Vetenskaps-Akad. Hand.*, 25, 1893. Id., Crinoidea, in *Lankester's Zoology*, Pt. 3, 1900 (Literature given). Reichensperger, "Anatomie von *Pentacrinus*," *Z.f.w.Z.*, 80, 1905, p. 22.

† In *Actinometra* the mouth is excentric, and the anus is nearly central.

calyx-cover between the ambulacral grooves are called the inter-ambulacral regions, and in one of these—the so-called posterior—is situated a papilla, at the end of which is the anus (Fig. 188). The stalk carries whorls of jointed appendages, the cirri; the segments to which such whorls are attached being called *nodal*, and the intervening segments *internodal*. In the unattached forms,

the apex of the calyx where the stalk would be attached, if present, carries more than one whorl of similar jointed cirri. The ambulacral grooves are continued from the calyx-cover along the whole length of the arms and their branches (excepting in a few cases, e.g. some of the posterior arms of *Actinometra* and some of the proximal pinnules of *Antedon*), and tube-feet project from their sides. As in Ophiurids the tube-feet are without ampullae and are not used as locomotive organs. The

arms and pinnules contain prolongations of all the most important organs of the calyx, excepting the alimentary canal, which as in Ophiurids is confined to the disc. The mouth is surrounded by small tentacles, the cavities of which open directly into the circumoral vessel of the water-vascular system.

Orientation and numbering of the rays. As stated above the interradius in which the anus is placed is called posterior. If the animal be drawn from the ventral surface with the anal in-

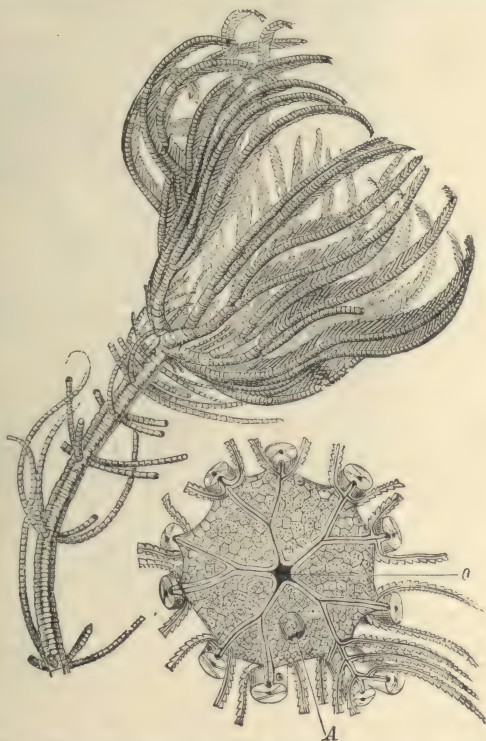


FIG. 187.—*Pentacrinus caput medusae* (from Claus, after J. Müller). O mouth; A anus. The lower figure is the tegmen calycis, the arms being cut off.

terradius downward in the figure, then in Crinoid nomenclature the three radii which project upwards constitute the trivium, the middle one being called anterior, while the two lower radii constitute the bivium. Further the right posterior radius is that radius of the bivium to the observer's right, the radius of the trivium on the same side being the right antero-lateral radius. On comparing this with the enumeration of the radii adopted in

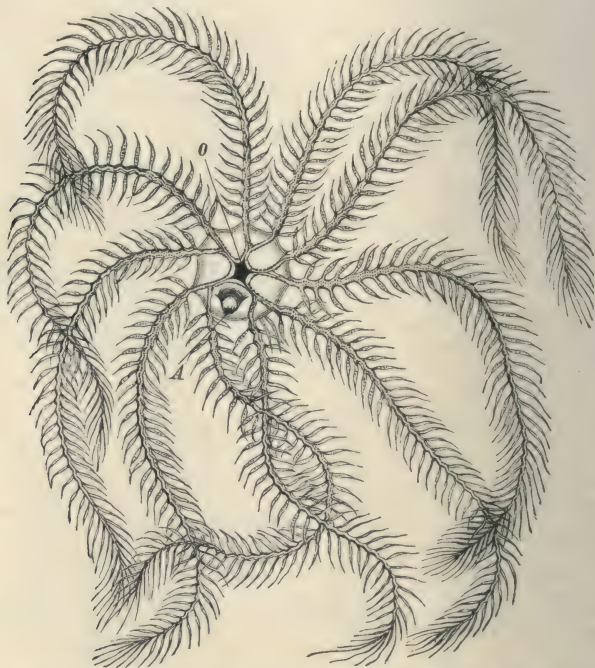


FIG. 188.—*Antedon bifida*, actinal surface (from Claus). O mouth, A anus. The pinnules are filled with the generative products.

this work (p. 119), it would appear that the right posterior radius would correspond to radius No. II, and the left posterior radius to radius No. III. Following out the same comparison the right antero-lateral radius of Crinoids is No. I of our enumeration, the anterior radius No. V, and the left antero-lateral No. IV. The use of the words *right* and *left* in this orientation is the exact opposite of their application in other Echinoderms.*

* As Lovén considers that the anus of Crinoids is in interradius V. I (as in exocyclic Echinoids), his nomenclature of the radii of Crinoids

Excepting for the anal interradius, which also contains the primary water-pore of the larva, pentameral symmetry of the Crinoid body is externally complete in almost all living Crinoids.* In extinct Crinoids, however, it is frequently disturbed by the insertion of the so-called anal plates in the posterior (anal) interradius. (See p. 276.)

As in most other Echinoderms the integument contains a large amount of calcareous matter in the form of, for the most part, regularly arranged plates, but movable spines † and pedicellariae are conspicuous by their absence.

The number of genera now living is comparatively small, but, judged from the Crinoid standpoint, their variation in structure is considerable; indeed, in this respect they may be said to be fairly representative of the immense number of forms which lived in the Palaeozoic epoch, when the group attained its greatest development. It is on account of these extinct forms that the study of the skeletal parts has attained in this class that relatively exaggerated importance which we found it to have in the case of Echinoids. It is a subject of great difficulty and the results arrived at, with regard to the structure of extinct forms, are constantly undergoing modification. Moreover the structure of the skeleton varies in closely allied forms in characters which it is customary to regard as having a high morphological value. For instance in the Camerate families Platycrinidae and Actinocrinidae the ambulacra of the calyx cover may be exposed or subtegmental even within the limits of the same genus (Wachsmuth and Springer), and the constitution of the apical system of plates may vary in the most important particulars in genera of the same family.

Crinoids have indirectly had an important influence upon our knowledge of the ocean. Until quite recently but two living genera of fixed Crinoids were known, *Pentacrinus* and *Holopus*. The discovery of *Rhizocrinus* in deep water by G. O. Sars in 1864, by the interest it excited on account of its stalked character and general resemblance to extinct forms, led to the expeditions of H.M.S. *Porcupine* in 1868, and H.M.S. *Lightning* in 1869,

would be as follows: right posterior radius = radius V, left posterior — radius I, anterior radius — radius III, and right antero-lateral — radius IV.

* *Thaumatoctrinus* is the most striking exception. see p. 301.

† Spines have been described in one extinct genus (*Arthrocantha*).

and the following years, and indirectly to the despatch of the *Challenger* expedition in 1872.

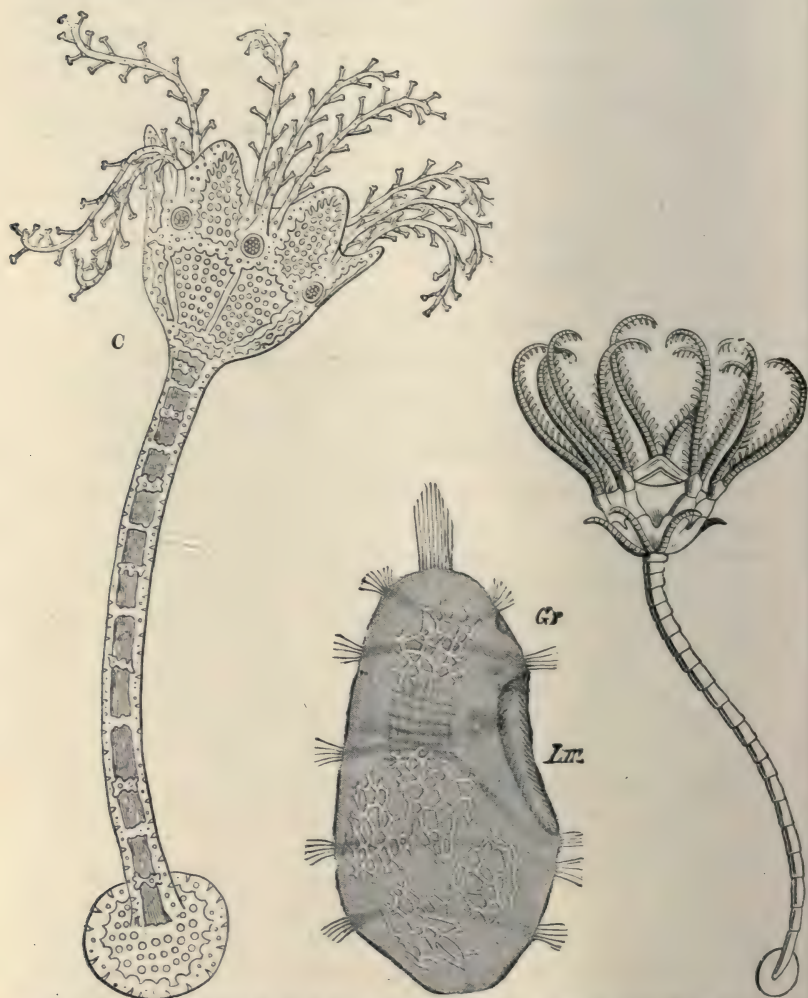


FIG. 189.—Developmental stages of *Antedon*, much enlarged (from Claus, after W. Thomson). *a* Free-swimming larva, with tufts and rings of cilia *Wr*, and with rudimentary calcareous plates. *b* Attached cystid stage of the same animal. *O* orals, *R* radials, *B* basals, *Cd* centro-dorsal plate. *c* older stage described as *Pentacrinus europaeus* with arms and cirri.

The general form of the body and skeletal plates of Crinoids may be considered under three heads: (1) the calyx and its cover, (2) the arms, and (3) the stem.

In the larva of *Antedon* and in what we may call the simplest forms—i.e. the Larviformia and *Marsupites* amongst extinct forms, *Holopus* and the Hyocrinidae amongst recent—the calyx is composed entirely of the plates of the apical system; whereas in the majority of Crinoids the lower ends of the arms are incorporated in it and together with some interradial plates assist in forming its walls. The apical system when fully developed consists of the following plates (Fig. 190): five

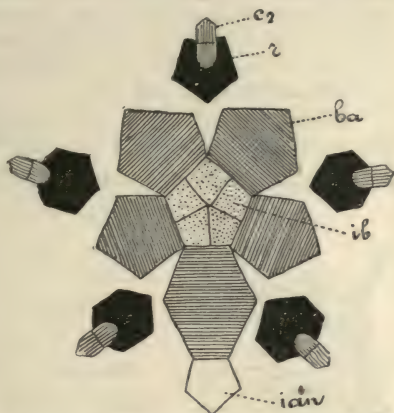


FIG. 190.—Analysis of the calyx of a dicyclic in-adunate form (from Lang). *ba* basal; *ib* infrabasal; *c2* second arm plate (primibrach 2); *ian* anal interradial (special anal).

infrabasals (*ib*) in contact at the apical pole and radial in position, five basals (*ba*) outside the infrabasals, in contact with each other, and interradial in position, five * radials (*r*) beyond the basals, in contact with each other and radial in position. Of these plates the infrabasals are sometimes absent, in which case the apical system is said to be monocyclic, as opposed to dicyclic when they are present.

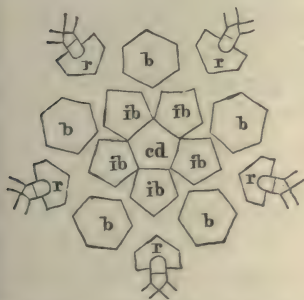


FIG. 191.—Analysis of the calyx of *Marsupites testudinarius* (from Zittel). *cd* central; *ib* infrabasal; *b* basal; *r* radial.

This character—the presence or absence of infra-basals—seems to be variable in most of the orders of Crinoidea. In the Flexibilia the base is said always to be dicyclic, but in the other orders both conditions are found. It is known that in many supposed monocyclic forms the infra-basals are really present in a reduced condition or have fused with the top joint of the stem (pseudo-monocyclic forms, e.g. *Antedon*). Wachsmuth and Springer assert that the mono- or dicyclic character of the calyx may be determined by inspection of the stem. In dicyclic

forms the lobes of the chambered organ are radial and the cirri are attached to the stem radially, and, if the stem be pentagonal, the angles are interradial; with monocyclic calices the reverse arrangement holds.

* Sometimes called *primary* radials.

In *Marsupites* there is a central plate in the middle of the five infrabasals (Fig. 191). There is a central plate also in the larva of *Antedon*, which however lie at the attached end of the stalk: it is called the **dorso-central** and was once supposed to be comparable with the central plate of other Echinoderms. It is not certain whether the central plate in the calyx of *Marsupites* is this plate or the top segment of a larval stem. In *Antedon* the central plate of the adult is a composite structure consisting of the top piece of the stem and the infrabasals: it is called the **centro-dorsal** (Fig. 189 Cd.).

The number of radials in the apical system is normally five, but the basals and infrabasals may be reduced to four, three or two.

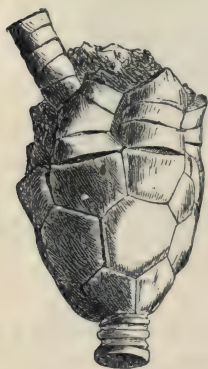


FIG. 192. — *Poteriocrinus* (after Zittel) showing a simple calyx with dicyclic base. There are two primibrachs but neither enter into the composition of the cup.

The reduction of the basals is supposed to be specially characteristic of the ancient Crinoids; all living Crinoids have five, except *Hyocrinus* which has three.* In living *Comatulidae* except *Atelocrinus* neither the radials nor the basals appear on the surface; the basals are united into a small plate, the *rosette plate*, which encloses the chambered organ. It frequently happens that the regular radial symmetry of these simple calyces is disturbed by the enlargement of the posterior basal and by the presence of an extra plate or of extra plates between the radials which border the posterior (anal) interradius (Fig. 190, *ian*). The anal interrarial plates have been much discussed.

When there is only one it rests upon the posterior basal and lies between the right and left posterior radials; it is called the **special anal** (Fig. 190, *ian*). When there is more than one, the lowest of them—that which intervenes between the radials and reaches the circle of basals—is called the **radial anal** (Fig. 201, *ra*), the rest being simply plates of the anal tube, of which the lowest is sometimes called the *special anal plate*. The irregularity of the calyx caused by this peculiarity of the anal interradius is never found in living forms † or in their allies, and was supposed to be generally characteristic of palaeozoic Crinoids. There are however, many of these in which it is not found.

* Fused to one in *Gephyrocrinus*, the ally of *Hyocrinus*.

† For the asymmetry of the living *Thaumatocrinus* see p. 301.

The origin of the radialian is supposed to be as follows. The right posterior radial (p. 272) is sometimes divided horizontally into an upper (oral) and lower (aboral) part. These are called the *superradial* and *inferradial* respectively. The inferradial is often shifted so as to lie in the anal interradius, between the right posterior radial (now superradial) and the special anal plate; it is then called *radialian*. This horizontal division of the radial may appear in other radii, but no shifting of the lower element occurs except in the radius specified.

The skeleton of the arms (Fig. 193). The arms are supported by a row of plates called *brachials*. They are placed on the abactinal side and are often grooved on their actinal or ventral

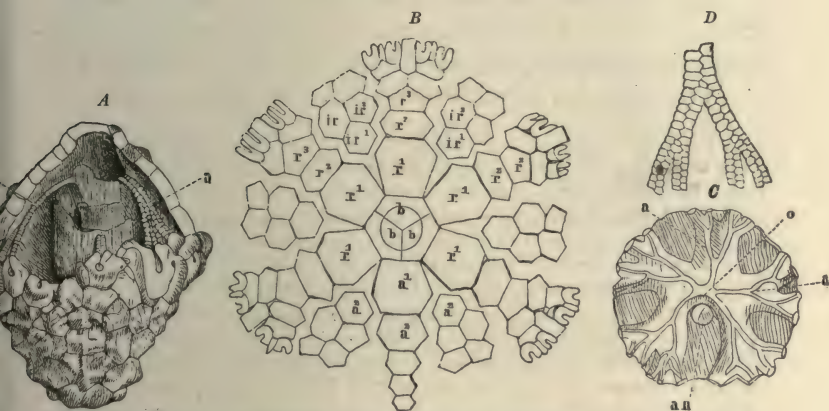


FIG. 193.—*Cactocrinus proboscidealis* Hall. Calcareous Limestone, Iowa. A, the calyx cover is broken away, so as to show the subtegmina skeleton; *a* the covering pieces of the ambulacral grooves. The opening of the ambulacral grooves are shown on the edge of the calyx at the ends of the rows of covering plates; the encroaching interambulacral plates are shown above the covering plates. B, analysis of the calyx (monocyclic); *b* basals; *r*¹ radials; *r*² primibrach; *r*³ axillary primibrach; *ir* interradians; *a*¹, *a*² anal interradian; the plates marked *a*² on each side of the anal interradian are interradians. C, cast of a calyx-cover showing the impressions of the ambulacral canals *a* leading to the mouth *o*; *an* anus. D covering plates of an ambulacral groove (from Zittel, after Meek and Worthen).

surfaces for the reception of the soft parts of the arms; moreover they contain a canal for the axial cord of the apical nervous system (Fig. 197, 8). The first brachial of an arm is carried by the corresponding radial plate of the apical system. When the arms divide once dichotomously, the brachials before the division are called *primibrachs* (*costals*) (Fig. 193, *r*², *r*³) and the brachial immediately before the division is called the *axillary primibrachial* or *primaxil* (*r*³). When the arms divide a second time the brachials which occur between the first and second divisions are called *secundibrachs* (*distichals*), the axillary secundibrach being

the *secundaxil*; and so on, *tertibrachs*, *quartibrachs* with *tertaxil*, *quartaxil*, etc., for the axillary pieces.

In Crinoids with a simple larviform calyx, viz. the Larviformia, some Fistulata, *Marsupites*, *Hyocrinus*, etc., the whole of the arm is free, no part of it assisting in forming the calyx. In this case all the brachials are said to be *free*. But in most Crinoids a certain portion of the lower part of the arm is incorporated in the calyx, which is thereby enlarged. In this case those brachials which are incorporated in the calyx are called *fixed brachials*. As a general rule when the calyx is thus enlarged a number of *interradial* plates are found in the wall of the calyx between the fixed brachials: these may be called *interprimibrachs*, *intersecundibrachs*, etc., according to their position between primibrachs, secundibrachs, etc. (Fig. 203).

In the Larviformia and Fistulata there are no interradian plates in the calyx excepting the anal plate or plates in the posterior interradius (Fig. 201). In *Thaumatocrinus* and the Rhodocrinidae there are five interradians regularly disposed around the calyx between the radials, and touching the basals; in *Thaumatocrinus* the anal interradius is marked by a short external jointed process. In the Camerata and Flexibilia, calyx interradians are generally present between the brachials (Figs. 193, 203), but not between the radials except in the Rhodocrinidae and except in the anal interradius, in which anal plates can often be made out. In the Articulata, calyx interradians are generally absent; they are present in some Apiocrinidae between the primibrachs, but are absent in the Encrinidae (Fig. 205), Bourguetierinidae, Pentacrinidae, and Comatulidae. In the Encrinidae no part of the arm is incorporated in the calyx, and in the last three families mentioned the body-wall which connects together those portions of the arms which are incorporated into the calyx resemble the calyx cover in either being without definite plates, or in having loosely arranged irregular plates. It thus appears that the radials form an uninterrupted circle in Articulata. In most other Crinoids they are interrupted in the anal interradius only, excepting in *Thaumatocrinus* and the Rhodocrinidae, in which they are interrupted in every interradius.

The brachial plates at the base of the arms are always in a single row, and in most Crinoids this arrangement is continued throughout the arms: this is the **uniserial** arrangement. But in some of the later palaeozoic forms the distal plates may be wedge-shaped, the broad end of the wedge being alternately on the right and left side of the arm: this is the **alternate** arrangement. Finally the plates may be in two series, the contact surfaces interlocking so as to give rise to a zigzag line; this is the **biserial** arrangement and often follows the alternate arrangement as the end of the arm is approached.

The **pinnules** are modified arm-branches. They alternate on the two sides of the arm and are often closely crowded. They contain all the organs found in the arms, are jointed like the

arms, and with the exceptions mentioned on p. 271 possess an ambulacral groove and tentacles. This view of them is suggested by their mode of origin in the growth of the arm, as branches at the growing end.* The first indication of a pinnule is the formation of a fork at the growing point of the arm; one of these branches grows faster than the other and forms the continuation of the arm, while the other becomes a pinnule. In *Hyocrinus* the proximal pinnules are almost as long as the arms and the pinnule-bearing joints have the appearance of axillaries. In the Cyathocrinidae there are no pinnules, but the arms are much branched and what would be pinnules in other forms are merely arm-branches.

The second brachial is the first arm joint which bears a pinnule (*Thaumatocrinus*, *Eudiocrinus*). Pinnules are always absent from axillary joints, from the hypozyal of every syzygy (see p. 283), and from the lower of every pair of joints that are united by ligamentous articulation.

The pinnules contain the generative organs, but the so-called oral pinnules of *Antedon* and its allies are sterile. In *Metacrinus* the ambulacral grooves of the proximal pinnules may start directly from the margin of the mouth or from the portion of the grooves on the calyx cover; so that the pinnules appear to be appendages of the calyx.

The **calyx-cover** (tegmen calycis) in the simplest cases consists only of the large triangular, interradially placed **oral plates** (sometimes called **deltoids**), which are arranged in such a manner as to form a pyramid-like projection over the ventral side of the calyx (Fig. 194). The outer sides of these plates are in contact with the radials of the calyx, and the posterior of them is, in *Haplocrinus* at any rate, perforated by the anus (Fig. 194). This arrangement is found in the Larviformia. In *Holopus* among living forms, a very similar condition is found, there being a very few small plates between the large orals and the edge of the calyx (the position of the



FIG. 194.—*Haplocrinus mespiliformis* from the posterior side. The anus is seen perforating the posterior oral and there is between the right posterior radial and the basals a plate which is the interradi- or radi-anal.

* In Comatulids, however, the proximal pinnules are formed later than the distal, and are not therefore formed at the growing point as arm-branches.

anus of *Holopus* is not known). In the living genera *Hyocrinus* and *Thaumatoocrinus*, the orals are very similar to those of the Larviformia, but between them and the edge of the calyx there are a few rows of interambulacral plates (Fig. 209). In *Rhizocrinus* also the orals are present, but much smaller than in those first mentioned, the part of the calyx-cover occupied by interambulacral plates being still more extensive.

In the Larviformia the oral pyramid is supposed to have been closed, the oral plates being actually connected with one another along the lines of contact, except at the base of the arms, where a small opening exists through which the ambulacral grooves pass out on to the arms. In such cases the mouth

is said to be **subtegminal**. This condition is not found in any living form: in *Holopus*, *Hyocrinus*, etc., the oral plates are not continuous and the mouth opens between them. But a very similar state of affairs is found for a short period in the development of *Antedon*. In the larva of this animal there is a stage in which the mouth surrounded by its fifteen tentacles opens into a closed sac, the *oral vestibule* in the walls of which are contained the

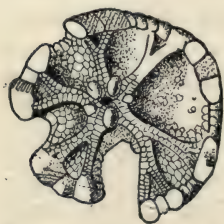


FIG. 195.—Calyx cover of *Taxocrinus intermedius* (after W. and Sp., from Delage and Hérourard).

large oral plates (p. 157). In the majority of forms, however, both living and extinct, the orals are either comparatively inconspicuous or absent in the adult.

In the Articulata (except *Rhizocrinus*) orals are absent. In the Fistulata they are distinct in some forms and not in others. When they are distinct they are in the centre of the calyx-cover and the posterior is the largest and is placed partly between the others. In some forms with subtegminal mouth (some Cyathocrinidae) the mouth is covered by 5 proximal ambulacral plates which simulate orals, the true orals (deltoids) being outside these. In the Flexibilia they are present in *Taxocrinus* and surround the open mouth (Fig. 195). In the Camerata they can generally be distinguished at the apex of the vault into which the calyx-cover is produced, but their identification is sometimes uncertain.

In the forms with small orals the greater part of the calyx-cover is occupied by compactly or loosely arranged **interambulacral** plates, which are continuous with the interradiial plates of the calyx, if such are present, and by the ambulacral grooves in their passage outwards to the arms.

The ambulacral grooves themselves are often protected by **covering plates** which arise at their sides and project over them : these could apparently be erected and depressed and are alternate on the two sides of the groove (Fig. 193, *A*, *D*, 195). The grooves are sometimes unprotected and open. In the Camerata it frequently happens that the interambulacral plates of the calyx-cover project over and cover up the ambulacral grooves (and their covering plates) which are thus converted into canals open at the edge of the disc where the arms are given off (Fig. 193, *A*). The mouth, being covered by the firmly united orals, communicates with the exterior, in such cases, only through these canals which branch as often as the arm branches before leaving the calyx. There is, however, as has already been stated, considerable variation amongst the Camerata with regard to this character.

Covering plates are found in some living forms, e.g. *Hyocrinus*, *Holopus*, Rhizocrinidae, some species of *Antedon*.

It appears, therefore, if the present accounts of Palaeontologists are to be trusted, that the mouth of the Camerata is, like that of the Larviformia, **subtegmental**. In both these groups, therefore, the only communication of the mouth with the exterior is by the ambulacral grooves which issue through openings between the bases of the central tegmental plates. In some Fistulata the grooves are open the whole way, and the mouth is not subtegmental; in others some of the central covering plates are enlarged and fixed, so that the grooves open immediately beyond them and the mouth is subtegmental. In some of the Camerata the ambulacral grooves open to the exterior only at or near the edge of the calyx (Fig. 193, *A*), the first part of their course being covered up by the encroachment of the interambulacral plates.

Further particulars as to the structure of the calyx-cover. In the Fistulata the calyx-cover is usually flat, except in the posterior interradius in which it is prolonged into an enormous sac-like process which no doubt contained a considerable part of the animal's viscera and had the anus at or near its apex. Both process and interambulacra generally are firmly plated.

In the Camerata the whole calyx-cover is symmetrically prolonged into a vault-like process (Fig. 202), at the end of which was the mouth covered up by the rather indistinct orals, and on the posterior side of which was the anus. The vault is firmly plated and its covering consists of the interambulacral plates and their extensions over the ambulacral grooves.

In the Flexibilia the calyx-cover is only known in *Taxocrinus*. It was flat and flexible with numerous loosely arranged interambulacral plates (Fig. 203). The ambulacral grooves are exposed and the orals are distinct and surround the freely open mouth.

In *Holopus* and *Hyocrinus* the structure of the calyx-cover has been sufficiently explained (p. 280). In most other recent forms the calyx-cover is membranous and has only loosely connected plates in the interambula-

era. The ambulacral grooves however have covering plates or, as in some Comatulids, covering folds without plates. The anus is at the end of a papilla in the posterior interradius, and its walls resemble in structure the interambulacral area from which it arises.

The covering plates of the ambulacral grooves are either attached to the brachials or to a special set of **lateral** or **side plates**.

The **stem** is composed of a number of ossicles united by close sutures or by articulation. It is traversed by an axial canal (see p. 288), and it may bear at intervals whorls of jointed cirri, which contain a prolongation of the axial canal. The cirri of the lowest pieces are in some forms root-like in appearance and ramify in the muddy or sandy bottom on which the animals live (*Rhizocrinus*); in this case the normal cirri may be absent. In other cases the lowest ossicle is attached to the substratum by a kind of cement (*Pentacrinus*). In growth the addition of new pieces is confined to the upper end of the stem, where they arise by intercalation between existing pieces and (except in Flexibilia and some Articulata) between the stem and the cup. In Flexibilia, etc., the top segment of the stem is often fused with the infrabasals..

In *Uintacrinus*, *Marsupites*, *Thaumatocrinus* and *Holopus* the stem is absent. In the Comatulidae it is present in the young, but in later life the animal breaks away from it, retaining only the top joint, on which several whorls of cirri are formed. This top piece (Fig. 189, *Cd*) which remains attached to the calyx in Comatulids may be formed of two or more joints fused, as is suggested by the numerous whorls of cirri on it; it is called the *centrodorsal* piece of the calyx and fuses with the infra-basals. It is uncertain whether *Thaumatocrinus* has a stem in the young state; probably it has. Whether *Marsupites* and *Uintacrinus*, which were also without stems, were fixed or not cannot be certainly determined. *Holopus* is attached by the broad base of its calyx, but it is without a stem.

The connexions between the skeletal pieces of Crinoids are of various kinds. In studying them it must be remembered that the plates are laid down as calcareous films in the connective tissue of the body, and that these, as they increase into plates, remain connected by the uncalcified connective tissue. When this tissue is well marked, the joint is said to be a *loose suture*; if it is contractile in function (muscular) we have a *muscular articulation*; such joints permit of movement of the connected plates on one another. When the plates are closely applied together and the intervening connective tissue is sparse, we have a *close suture*.

In a close suture, which is also called a *synostosis*, the plates are immovably connected together. A *syzygial* joint or suture, or a *syzygy* as it is sometimes called, is a close suture of two adjacent brachials, and is characterized by the fact that the proximal plate of the pair, i.e. the one next the calyx, does not bear a pinnule, while the distal one does. The proximal non-pinnuliferous piece of a syzygy is called the *hypozygal*, the distal one the *epizygal*. Syzygial suture is also found in the stem: in this case the lower piece of the pair or *hypozygal* is without cirri, while the upper piece or *epizygal* bears cirri. In *anchylosis* the plates are cemented together and the line of separation is difficult to distinguish or absent.

As in Ophiurids the ectodermal epithelium of the abactinal side of the arms and calyx is not to be distinguished. The epithelium of the ambulacral grooves is ciliated; elsewhere it is non-ciliated. The cutis contains the skeleton and its connective tissue is very largely replaced by calcareous plates.

There is no dermo-muscular system. The muscles are in bundles connecting the movably-articulated skeletal plates.

The **central nervous system** consists of a ventral ectoneural portion, a deep oral portion and a dorsal apical system.

The ventral ectoneural system (Fig. 197, 1) very closely resembles that of Asterids and as in them consists of an epithelial plexus, especially concentrated in the epithelium of the open ambulacral grooves of both arms and pinnules and of the ectoderm immediately surrounding the mouth opening.

The apical nervous system consists of a cap-like sheath of nerve fibres and cells surrounding the chambered organ (p. 288) and giving off interradially nerves, which bifurcate in the basals (*Antedon*, *Rhizocrinus*) or amongst the radials (*Bathocrinus*) into two strands, which diverge and pass to join the corresponding strands of neighbouring nerves (Fig. 196). The single cords so formed are radial in position and called the radial nerves of the apical system; they run to the tips of the arms and of their branches (Fig. 197, 8), and give off cords which similarly traverse the pinnules (Fig. 198). In the Articulata the whole system lies in canals—the so-called *axial canals*—in the skeletal pieces of the calyx and arms, viz. the infra-basals, the basals, the radials and the brachials. In some forms (*Antedon*, etc.) there is in the primaxil (Fig. 196, R_3) a chiasma and a commissure connecting the two nerves which result from the bifurcation of the main nerve, and the same nerves are in all cases connected, at the level of the radials, both with each other and with those

of adjacent radii by a commissure which forms a ring round the cup (Fig. 196).

In *Encrinurus* and *Pentacrinurus* the apical nerve cords are double. In many Palaeozoic Crinoids the canals for these axial cords are not separated from the ventral grooves on the brachials. In others they are present in the brachials, but exist only as grooves on the radials and basals.

The apical nerves give off branches which ramify in the ossicles (Fig. 197), and supply the muscles of the ossicles and the integument; some of them are connected with the branches of the deep oral system. A prolongation of the nervous sheath, which surrounds the chambered organ and forms the centre of this system, accompanies the prolongation of the chambered organ into the stalk and cirri, or if the stalk is absent into the cirri of the centro-dorsal plate.

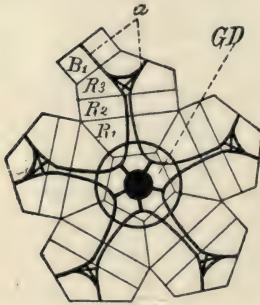


FIG. 196.—*Antedon bifida*. Diagram showing the arrangement of the apical nervous system in the calyx. *a* axial cords, the black disc in the centre of the figure represents the central sheath which surrounds the chambered organ; *CD* centro-dorsal plate; *B*₁ first secundo-brach; *R*₁ radial; *R*₂, *R*₃ primo-brachs (from Perrier after Ludwig).

As in Asterids the apical nervous system appears to originate in connexion with the coelomic epithelium. It was discovered by Dr. W. B. Carpenter* in *Comatula* as a result of his experiments on the animal. His observations were for some time discredited, but were eventually confirmed by Marshall,† who showed that the nervous aggregation round the chambered organ governs the movements of the arms and that the nerve cords proceeding from it contain both sensory and motor fibres.

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The deep oral nervous system is placed below the epithelium; it consists of a ring round the mouth and two radial nerves in each arm (Fig. 197, 4). The ring also gives off nerves which ramify in the connective tissue strands of the body-cavity. Branches of the brachial nerves of this system anastomose with branches of the apical cords.

Sense organs. There are no terminal tentacles nor special organs of sense. The tube-feet must be regarded as specially sensitive and possibly the whole arm as well. The tube-feet are supplied by both the superficial and the deep oral nervous system.

* *Proc. Roy. Soc.* 24, 1876, p. 211, and vol. 37, 1884, p. 67.

† *Q.J.M.S.*, 24, 1884, p. 507.

The **alimentary canal** is tubular and passes from the central or subcentral mouth to the excentric anus. In this passage it executes, in *Antedon*, one complete coil in the calyx. Its lining is ciliated and its central portion is slightly dilated. In some forms caecal outgrowths of the canal are present.

In *Actinometra* the digestive tube executes four complete coils in the calyx before the anus is reached. Moreover the mouth is excentric, being shifted anteriorly, while the anus is subcentral.

The **coelom** presents the usual division into perivisceral cavity and water-vascular system.

The perivisceral cavity occupies the calyx and extends into the arms. The calycine portion is for the most part traversed by a connective tissue network in which calcareous structures may be present. In some Comatulidae three parts of the body cavity may be distinguished. (1) an axial portion, in which there are no connective tissue strands; this occupies the axis of the calyx; (2) a perivisceral portion around the gut coils, and (3) a subcutaneous portion just beneath the integument and marked off from (2) by a kind of septum. These parts do not appear to have any special importance.

The perivisceral cavity is continued into the arms as three distinct sets of cavities, which however communicate at intervals. These are (Fig. 197), (1) the dorsal or coeliac canal (7), (2) the canal containing the generative rachis (6), and (3) the ventral or subtentacular canal (5). The last is divided by a septum into two, and on the dorsal wall of the dorsal canal depressed patches of ciliated epithelium are occasionally met with, especially in the pinnules. All these parts of the body-cavity are continued into the pinnules (Fig. 198), the only difference being that in the pinnules the generative rachis is swollen up into the generative glands.

The ventral canal, on reaching the calyx, opens into the axial part of the perivisceral space. The genital section is lost in the meshes of the body-cavity round the oesophagus, and the dorsal canal opens into the subcutaneous part of the body-cavity of the calyx. There is nothing corresponding to the axial sinus of Asterids and Echinids.

There is in the arms and pinnules a canal * (2) between the

* This canal is not always distinguishable. It may be due to shrinkage.

water-vascular trunk and the ambulacral groove which is supposed to represent the **perihæmal space** of other types. It appears to end blindly at each end, and there is no circumoral representative of it.

The **water-vascular** system consists of a circular vessel round the mouth giving off a radial vessel into each arm. The radial

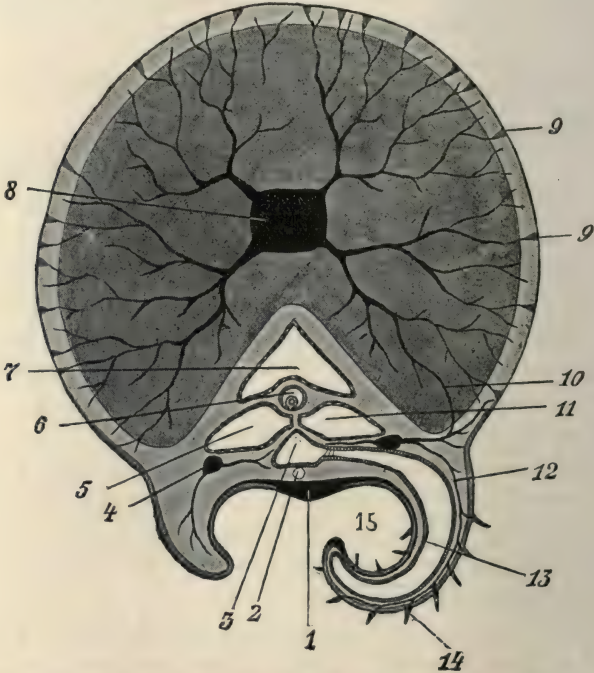


FIG. 197.—Diagram of a transverse section through the arm of a Crinoid (from Lang). 1 Radial nerve of the superficial oral system, 2 perihæmal canal (?), 3 radial water-vascular trunk, 4 the radial trunks of the deep oral nervous system, 5 and 11 the ventral or subtentacular canals, 6 the canal round the generative rachis, 7 the dorsal or coeliac canal, 8 radial trunk of the apical nervous system, 9 peripheral cutaneous termination of nerves of 8, 10 connecting nerve between 3 and 4, 11 subtentacular canal, 12 nerve to tube-foot, 13 water-vascular canal of tube-foot, 14 sensory process on tube-foot, 15 ambulacral groove.

vessels branch with the arms and extend into the pinnules. They terminate short of the end of the arms and there are no terminal tentacles. The water-vascular trunks have muscular walls and are sometimes traversed by muscular fibres. The lining epithelium is not, as in other Echinoderms, ciliated. The circular vessel gives off tubes which pass into the circumoral tentacles, and a number of other tubes which hang down and

open into the body-cavity. These are the representatives of the stone-canal of other types. They are usually very numerous and are without calcareous deposits in their walls. They open into the general body-cavity, the portion corresponding to the axial sinus of other types having become continuous in the adult with the perivisceral space. The calycine pores, each of which represents a madreporite of other Echinoderms, also open as we have seen into the body-cavity.

The radial canals give off lateral branches, each of which, in *Antedon*, supplies three tube-feet. In correspondence with this, the tube-feet are placed in groups of three at the sides of the ambulacral grooves and are without ampullae. They are to be regarded as purely sensory and respiratory structures, and are often called tentacles.

The water-pores are lined by a ciliated epithelium. In *Rhizocrinus lofotensis* there are only five, one in each interradius, and they open into the perivisceral cavity close to the opening of the stone-canals which are also five in number. In other Crinoids * the number of water-pores is very numerous (sometimes over 100), and it has not been shown that there is any relation between their openings and those of the numerous stone-canals. They are placed on the interambulacral portions of the calyx-cover, and they perforate the interambulacral plates if such are present. In *Actinometra* they have been observed on some of the proximal pinnules as well as on the calyx.

The **axial organ** (genital stolon) occupies the axial portion of the perivisceral cavity. Apically it has the form of a thin strand in the axis of the chambered organ; from this point it ascends in the body-cavity, where it widens. Its oral end is narrowed again to a few strands which are continuous (see below) with the generative rachis in the arms. It consists of convoluted canals lined by columnar epithelium and embedded in connective tissue of the vascular modification. The canals anastomose and end without leading to any organ.

The vascular system is present and has the usual form of anastomosing spaces in the mesoderm. It is richly developed in the wall of the alimentary canal, over the axial organ, in a ring round the mouth, and round the genital rachis and the genital

* In *Cyathocrinus* and other *Fistulata* there is said to have been a multiporous madreporite.

organs. It is not clear whether there is any radial branch of this system into the arms. The intestinal network and that over the axial organ communicates with the circumoral tract, and on the circumoral tract on the rectal side is a special development of this tissue containing cellular elements and called the *spongy organ*.

The chambered organ is a portion of the embryonic coelom (p. 156). In the adult it is completely cut off from the rest of the coelom and consists of five radially disposed chambers separated by interradiial septa, the whole being surrounded by the central organ of the apical nervous system (p. 283). It is placed at the apex of the calyx, in the Comatulids in the centro-dorsal plate. The chambered organ is continued, with its nerve investment, into the stalk in the stalked forms, and into the cirri if such are present.

The **sacculi** are globular sacs containing highly refractile spherules. They are found in the connective tissue at the edge of the ambulacral grooves of the arms, pinnules and calyx, and sometimes in other parts. Each spherule is in its origin related to one cell, the remains of which can be traced round it. Their meaning and function is unknown. They are absent in *Actinometra*, *Thaumatocrinus* and *Holopus*.

The **generative organs** may be described under two heads: (1) the generative rachis, and (2) the gonads. These two structures are continuous and form part of one structure of which the rachis is the sterile portion. The **rachis** is contained in the arms (Fig. 197): it is a cord of cells containing a small lumen and surrounded by vascular tissue. It lies in the genital division of the arm body-cavities and is continuous in the disc, through a circular cord (*Antedon*) or a network of strands (*Pentacrinus*), with the axial organ. The generative organs are developments of the terminal portions of the generative rachis, i.e. of the portion contained in the pinnules. In exceptional cases the generative rachis of the arms also gives rise to generative cells. In the pinnules the generative rachis swells up, its cavity becomes larger, and its lining cells become ova or spermatozoa (Fig. 198). These escape into the water probably by dehiscence.

So far as is known Crinoids are always of separate sexes, and the development, which has been followed in *Antedon* only

and is described at p. 152, takes place in the water and never in brood pouches.

Arms very readily break off so that the animals can escape if they become entangled or seized by enemies; the rupture takes place at a syzygy. Arms so lost are regenerated, but no cases of asexual reproduction have been met with. Regeneration of the viscera takes place after evisceration, and spontaneous evisceration is said sometimes to occur.

The number of radii, i.e. of primary arms, is nearly always five, but some extinct forms show indications of having had a different number, e.g. Plicatocrinidae with 4, 6, or 8 (rarely 5 or 7) radials.* Moreover specimens of *Rhizocrinus* are found with 4, 6, or 7 radii, and of the few specimens of *Holopus* (Fig. 210) that have been found one was tetramerous. Among Comatulæ also forms with 4 and 6 rays are very rarely met with.

Except in *Rhizocrinus*, it is rare to find the number five departed from.

The Crinoids, especially those living near the shore and to a depth of 150 fathoms are gregarious in their habits, and the remains of the Crinoid forests in the Silurian and Carboniferous rocks show that this habit is not confined to living forms. In the Crinoid forests found in Palaeozoic rocks different genera and species, belonging even to different orders, are associated. whereas after Palaeozoic times the Crinoid forests consist of associations of individuals of the same species. *Antedon* (Fig. 188) is free but can anchor itself by its cirri; *Rhizocrinus* (Fig. 207) is attached by a branching root, while the lowest joint

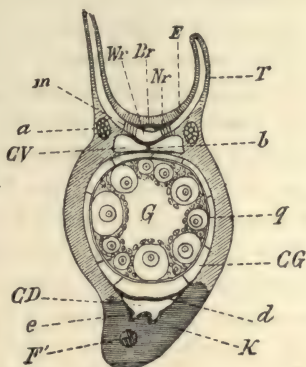


FIG. 198.—Transverse section through a pinnule of an adult female of *Antedon* (after Ludwig). *a* sacculus; *b* septum between the subtentacular canals; *Br* periaermal canal; *CD* coeliac canal; *CG* genital canal; *CV* subtentacular canal; *d* membrane separating the coeliac canal from the genital canal; *e* ciliated pit of the coeliac canal; *E* epithelium of ambulacral groove; *F* trunk of apical nervous system; *G* cavity of the ovary; *K* calcareous plate; *Nr* radial nerve; *q* membrane enveloping the ovary; *T* tentacles (tube-feet); *Wr* radial water-vascular canal.

* The living *Promachocrinus* is peculiar in having 10 radials.

of the stem of *Pentacrinus* (Fig. 208) is attached to the substratum, but this attachment may be lost by the breaking of the stem or other cause, and the animal may move freely, anchoring itself by its stalk cirri like an *Antedon*. Locomotion in the case of *Antedon* is effected by the movement of the arms. It is possible that some of the extinct forms, e.g. *Marsupites*, and *Uintacrinus* were free.

Food is brought to the mouth by ciliary currents along the arm grooves in the form of floating organisms. The principal external parasite is *Myzostoma* (vol. I, p. 492), which infests the disc, stalk and arms often in great numbers; it may be free or enclosed in a cyst in the body wall.

The class Crinoidea is divided into five orders, Larviformia, Fistulata, Camerata, Flexibilia, and Articulata. The living forms are all contained in the order Articulata.

The grouping of Crinoids into Palaeocrinoids comprising the Larviformia, Camerata, Flexibilia and Fistulata, and Neocrinoids (Articulata) must be given up. As in the case of Echinoids the living forms interdigitate with the extinct. The most important character of extinct forms not found in the living is the pentameral asymmetry of the calyx brought about by the presence of interradianal plates in the posterior interradius, but this is by no means shared by all the Palaeocrinoids (Platycrinidae, Calyptocrinidae, etc.) and indications of it are present in the jointed process of the posterior interradius of the living *Thaumatocrinus*. As stated above, the forms grouped under our order Articulata are, with the exception of this character, a very fair sample of all Crinoids that are known.

The following are some of the characters which were considered to mark the ancient forms.

In the Palaeocrinoids in which some of the arm plates (above the radials of the calyx) enter into the composition of the calyx, the plates which are so absorbed are united by interradianally placed plates (interprimibrachs etc.); in Neocrinoids when the lower arm joints are so taken into the disc, there are usually no interradianal plates between them, the arm plates being in contact or the intervening body wall flexible; though this does not hold in all cases, e.g. *Apiocrinus*, *Guetardicrinus*, *Uintacrinus*. The perforation of the radials by the axial cord is also said to be a characteristic of the Neocrinoids. In most Neocrinoids with divided arms, the axillary is the second primibrach (*Metacrinus*, *Plicatocrinus* excepted), while in Palaeocrinoids the axillary varies from the radial to the 6th primibrach—this is the only important character which separates the Palaeocrinoids *Erisocrinus*, *Phialocrinus* and *Stemmatocrinus* from *Encrinus*.

Affinities. The Crinoidea stand far apart from the other classes of living Echinodermata. Their important distinctive

characters are as follows. (1) They are all, with the partial exception of the Comatulids and possibly one or two others, attached throughout life, and the oral pole which also carries the anus is turned upwards. (2) The gonads are removed altogether from the disc and lie in the ultimate branches of the arms. (3) The anterior coelom becomes merged in the general perivisceral cavity, and there is no axial sinus in the adult. (4) The anterior coelom is given off from the enteron separately from the posterior. (5) The absence of any trace of a right hydrocoel. (6) The fact that the oral surface of the adult is derived from the posterior surface of the larva. (7) The form of the larva. (8) The open condition of the ambulacral grooves. Some of these are absolutely distinctive, viz. (4), (6), (7). Some of them are shared either wholly or partly by Asteroids, viz. (1), (2), (8). Holothurians present (3), and so far as is known (5). The bias is therefore on the whole towards Asteroids, as we have already pointed out in discussing the affinities of Holothurians, but the bias is very slight, for (8) cannot be regarded as an important character seeing that Ophiuroids, so closely related to Asteroids, do not share it, and (2) is partly shared by Echinoids, so far as the pentamerous arrangement of the gonads is concerned. So that (1) only is left. But this resemblance carries with it an important difference. It is true that Asteroids are the only living Echinoderms outside the Crinoids which present fixation at any time of life and that the fixation is effected by the preoral lobe, but as shown by MacBride there is this important difference: whereas in Asteroids the pedicle of attachment is found to arise from the oral surface of the adult and is surrounded by the hydrocoel ring (Fig. 105), in Crinoids it springs from the aboral surface and is outside and far removed from the circumoral water-vessel. This discrepancy undoubtedly receives its explanation by a consideration of the fact that fixation takes place in both classes some time before the hydrocoel ring becomes complete. But it is none the less significant, especially when taken in conjunction with another fact. In all Echinoderms the mouth shifts during the development. In all classes except Crinoids it shifts on to the left side, so that the left side or left ventral side of the larva becomes the ventral side of the adult. In Crinoids however it shifts further; not only does it move on to the left side indenting the left hydrocoel

and the left posterior coelom, but it continues its movement, carrying with it the left coelom and hydrocoel, until it comes to lie beside the anus at the posterior end (see account of development). Having reached this point, far removed from the preoral lobe, the hydrocoel ring closes. As a result of this movement, which must be due to a torsion of the whole of the posterior part of the body, the right posterior coelom has also shifted and come to lie on the aboral (originally anterior) side of the gut, and the preoral lobe of the larva becomes enclosed by the row of skeletal elements (apical plates) which are developed outside the right posterior coelom in all Echinoderms except Holothurians. These plates as is well known are laid down at first in the larva in an open curve, which later closes, as does the hydrocoel, to form a complete ring. In Asteroids the closure of this curved row of plates is effected far from the point of origin of the preoral lobe, on the right or right dorsal (larval) side of the body. In Crinoids it is effected at the anterior (larval) end of the body and encloses the preoral lobe, just as the hydrocoel does in Asteroids. If these considerations are sound, it follows that the rejection of the hypothesis as to the homology between the apical plates of Crinoids and those of other Echinoderm classes, in so far as that rejection depends upon the difference in the point of origin of the stalk in Asteroids and Crinoids, is not justified.

The fact that in Crinoids alone is the rudiment of the posterior coeloms given off at the posterior end of the larva and separately from that of the anterior becomes to a certain extent intelligible in view of the foregoing considerations. This peculiarity must be regarded as a back-thrust from the adult form, in which the posterior end comes to hold all the viscera. Pursuing the same line of thought the fact that the hydrocoel does not share in this impress of adult arrangements and in like manner develop from the posterior end of the enteron but comes off in front with the anterior coelom is significant as showing that the connexion in origin of the hydrocoel and anterior coelom is a fundamental feature of Echinoderm morphology.*

The fact that the left posterior coelom does not at an early stage come to exceed the right in size is another feature of the larva of

* This holds even in Ophiurids, see p. 151, and MacBride, *Q.J.M.S.* 51, 1907, p. 557.

Crinoids in which they differ markedly from Asteroids, though not so far as is known from other classes.*

Order 1. LARVIFORMIA (*Inadunata larviformia* Wachsm.)

The calyx-cover consists entirely or almost entirely of five triangular oral plates which are applied together so as to form a pyramid and cover the ambulacral grooves of the disc as well as the mouth.† The calyx is monocyclic and consists of basals and radials only except in Cupressocrinidae and Stephanocrinidae, there being no interradiial plates except in the anal interradius. The anal interradius is frequently unlike the other interradii. The plates are immovably connected by smooth sutural surfaces. The arms are weak† and entirely free. The large orals and simply constructed calyx are characteristic of larvae of living Crinoids. Upper Cambrian to Carboniferous.

Fam. 1. **Haplocrinidae.** Calyx small, irregular, with five unbranched arms. Some of the radials are composed of two pieces (Fig. 199). Anus is in the posterior oral. *Haplocrinus* Steininger (Fig. 199), Devonian.

Fam. 2. **Allagecrinidae.** Calyx small; basals and radials 5. Oral plates triangular. *Allagecrinus* Eth. and Carp.

Fam. 3. **Pisocrinidae.** *Pisocrinus* de Kon. *Triacrinus* Münst.

Fam. 4. **Symbathocrinidae.** *Symbathocrinus* Phillips, *Phimocrinus* Schultze, *Stylocrinus* Sandb., *Stortingocrinus* Schultze, *Lageniocrinus* de Kon.

Fam. 5. **Cupressocrinidae.** Calyx pentamerally symmetrical, 5 basals, 5 radials, no interradials. The basals surround a pentagonal centro-dorsal plate (? top segment of stalk). 5 broad and thick arms, which are traversed by a nerve canal. *Cupressocrinus* Goldfuss, Devonian.

Fam. 6. **Stephanocrinidae.** Calyx composed of 3 high basals, 5 deeply forked radials, and 5 small interradials; with branching arms (each arm-joint gives off side arms which are non-pinnulate). U. Cambrian, Silurian. *Stephanocrinus* Conrad.



FIG. 199.—*Haplocrinus mespiliiformis* (from Delage and Hérouard, after W. and S.), from the anal side.

Order 2. FISTULATA (*Inadunata fistulata* W. and S.)

Calyx covered with thin plates which easily fall apart from one another and may be prolonged in the anal interradius into a usually high balloon-shaped, or short conical tube. The ambulacral furrows are covered by alternating covering pieces but are not subtegmina. The mouth is eccentric and sometimes subtegmina (see p. 280). Basals and radials of the calyx immovable, connected by simple suture. Arms free, no brachial included in the calyx, uni- or bi-serial, usually branched, the segments connected by simple sutures, with or without pinnules. Interradiial anal plates may be present in the anal interradius, one of them

* It is somewhat surprising, having regard to their early inequality in Asteroids, that in Holothurians and Echinoids, in which the ambulacral surface of the adult so much exceeds in area the antambulacral, the right and left posterior coeloms should remain approximately equal in size in the larva.

† Exception Cupressocrinidae.

being usually a radianal, and another a special anal (p. 276). U. Cambrian to Permian. Other interradials are not present.

Fam. 1. **Hybocrinidae**. Monocyclic, 5 high basals. The right posterior radial compound; the superradial small or absent, the interradial (radianal) large. Arms simple unbranched, uniserial. *Hybocrinus* Billings, *Hoplocrinus* Grewingk. *Baerocrinus* Volborth.

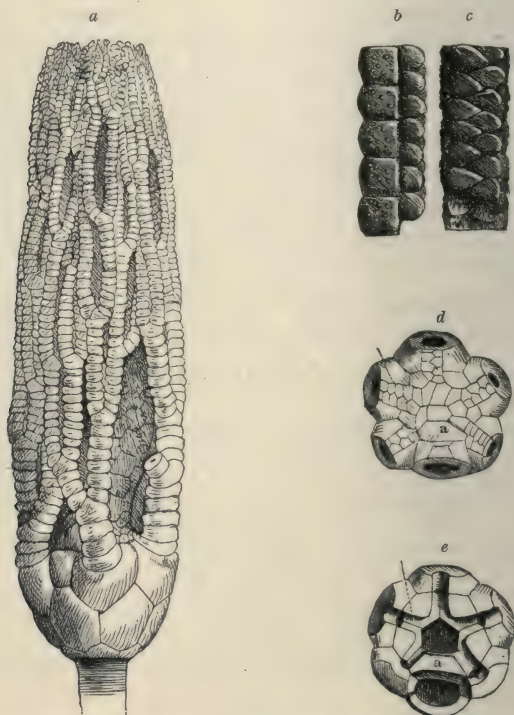


FIG. 200.—*Cyathocrinus longimanus* Ang. (from Zittel). *a*, calyx with arms, nat. size (after Angelin). *b*, arm fragment of *C. ramosus* Ang. from the side, *c* from above (showing the covering plates). *d*, calyx cover of *C. malvaceus* Hall; *e* the same after removal of the calyx plates which lie on the interambulacral plates (after Meek and Worthen).

Fam. 2. **Heterocrinidae**. Monocyclic, 5 basals, some of the radials consisting of 2 pieces connected by a horizontal suture. Arms uniserial, branched. *Heterocrinus* Hall, *Ihocrinus* Hall, *Ohiocrinus* Waschm.

Fam. 3. **Anomalocrinidae**.

Fam. 4. **Belemnocrinidae**.

Fam. 5. **Catilloocrinidae**.

Fam. 6. **Calceocrinidae**.

Fam. 7. **Gasterocomidae**. Dicyclic, Infrabasals fused into a disc. With one interradial anal plate. Anal opening low down above the anal plate and between two radials. *Gasterocoma* Goldf., *Myrtillocrinus* Sandb., *Nanocrinus* Müll.

Fam. 8. **Cyathocrinidae**. Dicyclic (Fig. 190). 1 or 2 interradials in the

anal interradius and often a radial. 5 oral plates and high ventral tube. Arms long, much branched, uniserial, without pinnules. U. Cambrian to Carboniferous. *Cyathocrinus* Miller (Fig. 200), *Barycrinus* W. and S., *Homocrinus* Hall, *Lecythocrinus* Mull., *Arachnocrinus* M. W., *Gissocrinus* Ang., *Porocrinus* and *Carabocrinus* Billings.

Fam. 9. **Crotalocrinidae.** Dicyclic; calyx of 5 infrabasals, 5 basals, 5 radials, and a small anal interradial. Lower brachials laterally in contact. Arms much branched, and branches connected. No pinnules. Axial canals in arm-plates. Silurian. *Crotalocrinus* Austin, *Enalocrinus* d'Orb.

Fam. 10. **Poteriocrinidae.** Dicyclic. 5 infrabasals sometimes hidden by the column, 5 basals, 5 radials; 1-2 interradial anals and often a radial. Ventral sac large. Arms simple or branched, with long pinnules; uniserial, alternate, rarely biserial, Devonian and Carboniferous. *Poteriocrinus* Miller (Figs. 192, 201), *Woodocrinus* de Kon., *Scaphiocrinus* Hall, *Agassizocrinus* Troost, *Cromyocrinus* and *Phialocrinus* Trautsch., *Erisocrinus* M.W., *Stemmatocrinus* Trautsch. In the last two genera the interradial plate of the anal interradius is very small or absent.

Order 3. CAMERATA.

The calyx is enlarged by the incorporation of the proximal brachials: * it consists of a monocyclic or dicyclic base, a circle of radials, and of a certain number of the proximal brachials. The latter are connected by interradial (interbrachial) plates; the plates of the anal interradius being more numerous than the others. The radials are in contact all round (*Melocrinidae*, *Calyptocrinidae*, *Platycrinidae*); they are separated only in the anal interradius by an anal plate (*Thysanocrinidae*, *Batocrinidae*, *Actinocrinidae*, *Crotalocrinidae*, *Hexacrinidae*); they are separated all round (*Rhodocrinidae*). Infrabasals are present or absent. The calyx-cover is a vault of solid plates firmly connected together. The mouth is central and covered with 5 firmly united oral plates the hindmost of which is often the largest and projects in between the four others. The orals are sometimes quite inconspicuous. The interambulacral plates of the calyx-cover sometimes project over and cover the ambulacral plates (Fig. 193). The mouth being covered up by the orals, its only communication with the exterior is through the ambulacral canals, which open at the base of the arms and branch as often as the arms branch before leaving the calyx. Anus excentric or subcentral, often at the end of a proboscis-like prolongation. The plates of the calyx are connected by simple, smooth sutural surfaces. They are sometimes continued without any break into the interambulacrals of the calyx-cover. Arms with one or two rows of brachials, usually with pinnules. Dorsal canals have not been observed in the brachials. U. Cambrian to Carboniferous.

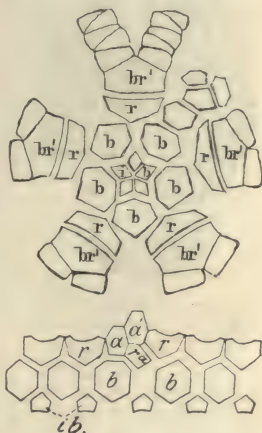


FIG. 201.—Analysis of the cup of *Poteriocrinus* (from Zittel, after Bather). *a* special anal, *a'* interradial anal, *ra* radial, *b* basal, *ib* infrabasal, *br'* primibrach.

* Except in some *Platycrinidae*.

Fam. 1. **Platycrinidae**. Calyx formed of a monocyclic base and a circle of 5 large radials. Interradials restricted almost exclusively to the calyx-cover, which consists of firmly connected, usually thick plates and is usually much arched (Fig. 202). No anal plate. Arm-branches 10, 20 or more, generally free from the distichals upwards. There is one primibrach

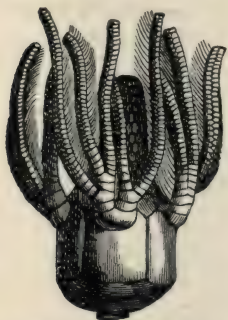


FIG. 202.—*Platycrinus trigintidactylus* (restored after de Koninck from Zittel).

(Br. 1) attached to the radial; the following brachials are free and the arm branches close to its base. Pinnules well developed. The covering plates of the ambulacra are often exposed on the surface of the calyx-cover. Silurian to Carboniferous. *Platycrinus* Mill. (Fig. 202), Carboniferous, *Marsipocrinus* Bather, *Culicocrinus* J. Müll., *Cordylocrinus* Ang.

Fam. 2. **Hexacrinidae**. Monocyclic, 2 or 3 basals, first anal plate resting on basals and similar in form to radials. Other plates as in *Platycrinidae*. Devonian and Carboniferous. *Dichocrinus* Münster; *Arthracantha* Williams (*Hystericrinus* Hinde), calyx plates beset with mobile spines. *Hexacrinus* Austin, *Talarocrinus* W. and Sp.

Fam. 3. **Actinocrinidae** (Fig. 193). Monocyclic. Calyx composed of 3 basals, 5 radials, 5×2 primibrachs, and $5 \times$ a variable number of secundibrachs. First anal interradial plate resting on basals, the other first interradials upon the radials. Arms 5 to 30 or more, uni- or bi-serial with long pinnules. Calyx-cover usually much arched and ambulacra of disc hidden by interambulacral plates. With or without anal tube. U. Cambrian to Carboniferous. *Carpocrinus* Müll. *Actinocrinus* Mill. *Cactocrinus* W. and Sp. (Fig. 193). *Strotocrinus* M. and W. *Batocrinus* Casseday. *Dorycrinus* Roem. *Desmidocrinus* Ang. *Agaricocrinus* Troost.

Fam. 4. **Barrandocrinidae**. Monocyclic, 3 basals. Arms biserial, laterally fused with each other, and bent back so as to lie with their dorsal sides against the calyx. Silurian. *Barrandocrinus* Ang.

Fam. 5. **Reteocrinidae**. Monocyclic or dicyclic. Infrabasals when present 5, basals 4 or 5. Radials separated by a large special anal which supports a vertical row of anals. The spaces on either side of this row, as well as the other four interradia paved with minute pieces. U. Cambrian. *Reteocrinus* Bill. *Xenocrinus* Miller.

Fam. 6. **Thysanocrinidae**. Dicyclic, radials in contact laterally except at the posterior side, where they are separated by an anal plate, U. Cambrian, Silurian. *Dimerocrinus* Phill. (*Glyptaster*, *Thysanocrinus*, *Eucrinus*). *Cyphocrinus* etc.

Fam. 7. **Rhodocrinidae**. Dicyclic. Calyx composed of 5 infrabasals, 5 basals, 5×2 primibrachs and $10 \times 1-3$ secundibrachs; interradials numerous. The first interradials inserted between the radials and touching the basals. The anal interradius is hardly distinguished from the others. U. Cambrian to Carbon. *Lyriocrinus* Hall, *Rhipidocrinus* Beyrich, *Rhodocrinus* Miller.

Fam. 8. **Melocrinidae**. Monocyclic, 3-5 basals, radials in contact all round, neither anal nor interradials touching the basals, 2×5 primibrachs, and 2 to 3×10 secundibrachs. Arms 5×2 with secondary branches which bear the pinnules. U. Cambrian to Devonian. *Melo-*

crinus Goldf. (*Otenocrinus* Bronn), *Xenocrinus* Miller, *Patellioocrinus* Ang., *Glyptocrinus* Hall, *Corymbocrinus* Ang. (*Polypeltes* Ang.), *Stelidioocrinus* Ang. (*Harmocrinus* Ang.).

Fam. 9. **Calyptocrinidae.**

Monocyclic. Calyx regular, composed of 4 basals, 5 radials in contact, 2×5 primibrachs, 5 secundibrachs; all interradii alike. Arms 20, biserial. Silurian, Devonian. *Callicrinus* Ang., *Eucalyptocrinus* Goldf., *Hypanthocrinus* Phill.

Order 4. **FLEXIBILIA.**

Calyx cover flat, flexible, with loosely arranged interambulacral plates. Ambulacra with alternating covering plates, their calycine portions apparently not covered by interambulacral plates (Fig. 195). Mouth central, open, surrounded by 5 orals. Anus excentric. Dicyclic, 3 or 5 small infrabasals, often hidden by top joint of stalk. The calyx extends to the lower brachials (primibrachs, secundibrachs and sometimes terti-brachs being included) and the brachial plates of the calyx are united by articulation, not by suture. The brachials incorporated in the calyx are either in contact laterally or separated by interradials extending to the basals or first radials. A single azygos (anal) plate sometimes present in the posterior interradius. Arms strongly branched distally, uniserial

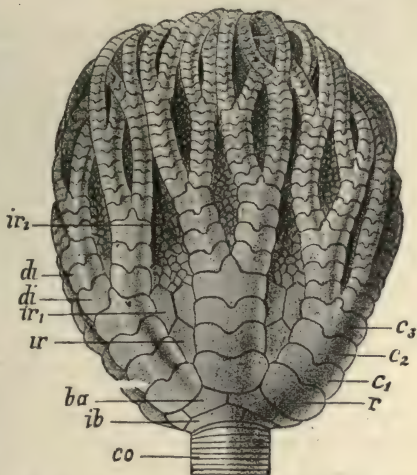


FIG. 203. — *Taxocrinus splendens* Mill. and Gurley (from Lang). *ir*, *ir1*, *ir2* interradials, *di* secundibrachs (distichals), *ba* basals, *ib* infrabasals, *co* stalk, *r* radials, *c1*, *c2*, *c3* primibrachs (costals).



FIG. 204. — *Marsupites testudinarius* Schloth. (after Zittel). *a* calyx, nat. size; *b* radial with the first arm segment; *c* upper part of arms.

with or without pinnules. All brachialia with dorsal canal (except sometimes in the distal brachials), and united by articulation. U. Cambrian to Carboniferous.

Fam. 1. **Ichthyocrinidae**. With characters of order. *Ichthyocrinus* Conrad, *Lecanocrinus* Hall, *Taxocrinus* Forbes (Fig. 203), *Forbesiocrinus* de Kon.

The following genera are allied here :

Marsupites Mant. (Fig. 204), Upper Cretaceous of Europe and Asia. Calyx dicyclic, large, unstalked, composed of large thin plates, viz. central (? centrodorsal), 5 infrabasals, 5 basals and 5 radials (Fig. 191). Interradials and anals absent. Arms entirely free, branched, uniserial with dorsal canal.

Urtocrinus Grinnell. Calyx pseudo-monocyclic, symmetrically pentamerous, unstalked, composed of thin plates. Infrabasals sometimes preserved, but usually atrophied. 5 basals enclosing a small pentagonal centrodorsal, 5 radials, and 5×2 primibrachs. The axillary primibrach carries two rows of secundibrachs which gradually pass into the arms. Intersecundibrachs, usually 2, may rise to 8. Arms long, thin, uniserial, with numerous pinnules, connected over the calyx wall by large inter-brachials. Upper Cretaceous of Kansas and Westphalia.

Order 5. ARTICULATA J. Müll. (*Neocrinoidea* P. H. Carp. *Canaliculata* Chapman.)

Calyx-cover membranous, or with usually flat, loose plates. Ambulacral furrows and mouth open. Orals are present in the young state, and sometimes in the adult. Calyx regular (all interradii alike), pseudo-monocyclic (i.e. the infrabasals usually not separate, but atrophied or fused with the top stem-joint); 5 basals sometimes not visible externally; radials laterally in contact except in *Thaumatoocrinus*. 5×2 primibrachials. Anal plates always absent. Interradials rarely present. Arms branched or unbranched. Stalk probably always present in the young, but absent in some adults. Basals, radials and brachials perforated by dorsal canals. Arms (with one exception) uniserial or alternate, with pinnules.

Trias to present time. The group includes all living, tertiary, and mesozoic Crinoids except *Marsupites* and *Urtocrinus*. They are mainly characterized by the open mouth and ambulacral grooves and by the dorsal canal in the arm plates.

Fam. 1. **Encrinidae**. Calyx dicyclic, 5 small infrabasals stuck on to the top stem-joint, 5 basals, 5 radials, interradials absent. Calyx cover arched and plated. Arms divide once or twice, close together, biserial or alternate. Trias. *Encrinus* Miller (Fig. 205).

Fam. 2. **Apiocrinidae**. Calyx regular, composed of very thick plates, 5 large basals, primibrachs 0 or 2×5 , and sometimes secundibrachs. Pseudomonocyclic, the infrabasals being fused with the centrodorsal. Interradials are sometimes present, but above the radials. Calyx cover plated. Arms branched with



FIG. 205.—*Encrinus liliiformis* (from Claus).

long pinnules. Stalk long, circular, rarely pentagonal, without cirri often much expanded near the calyx. Jura, Chalk, present day. *Apiocrinus* Miller, f; *Guetardocrinus* d'Orb., f; *Millericrinus* d'Orb., f; *Acrochordocrinus* Trautschold, f; *Calamocrinus* A. Ag.* recent, Galapagos Island.

* A. Agassiz, *Calamocrinus diomedae*, Mem. Museum Comp. Zoology, 1892.

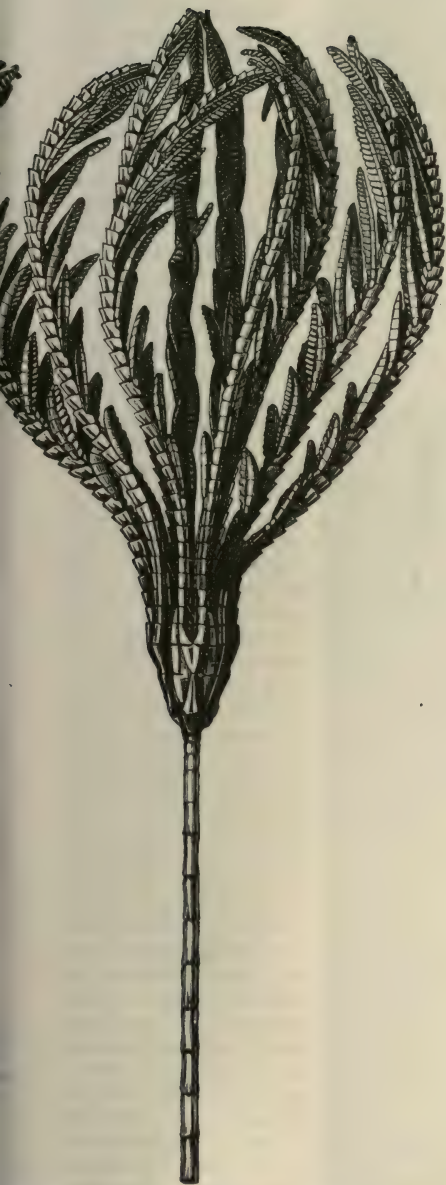


FIG. 206.—*Bathyrinus aldrichianus*, W. Thomson $\times 3$ (from W. Thomson).

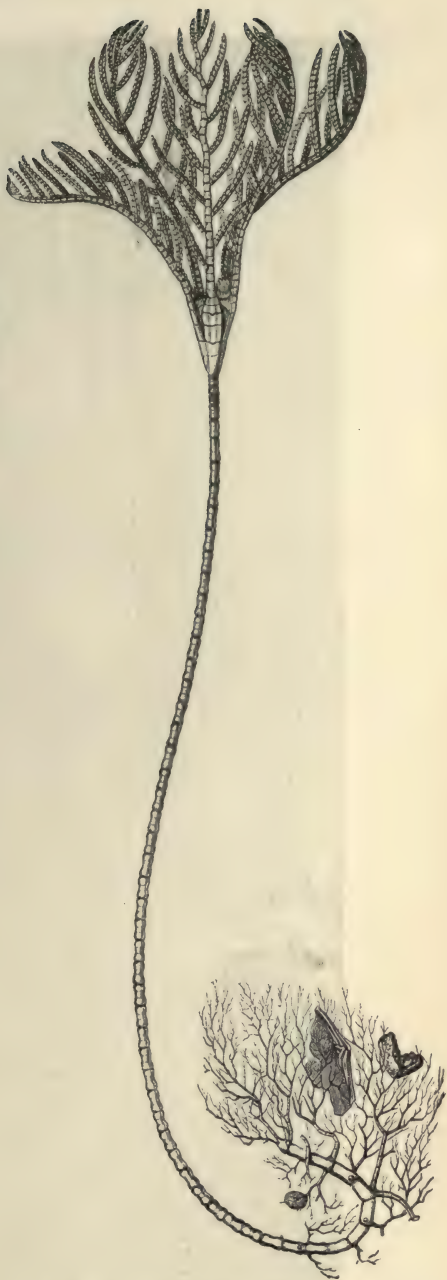


FIG. 207.—*Rhizocrinus lofotensis* M. Sars. $\times 1\frac{1}{2}$.

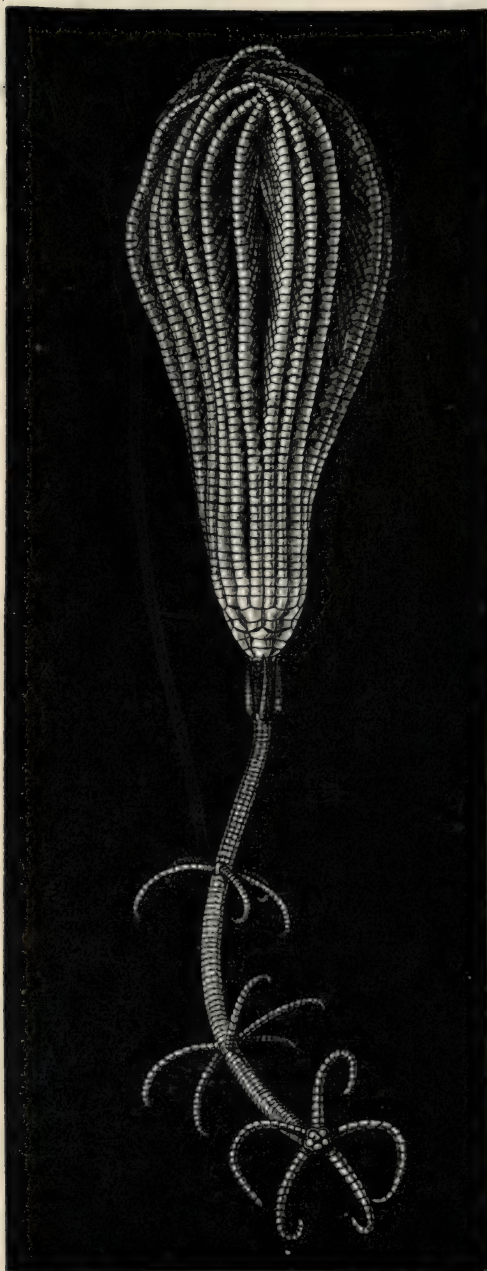


FIG. 208.—*Pentacrinus wyville-thomsoni* Jeffreys, nat.-size (from Wyville Thomson).

Fam. 3. **Bourgueti-**
crinidae. Calyx small, consisting of 5 basals, 5 radials, and sometimes 2×5 primibrachs. Calyx cover membranous with 5 orals. Ambulacra with covering plates, but without side plates. Stem with branching root. Jurassic to present time. *Bourguetocrinus* d'Orb, Tertiaries; *Rhizocrinus* Sars (*Conocrinus* d'Orb.), the arms are very variable in number, out of 75 specimens examined by Sars, 15 had 4 arms, 43 had 5, 15 had 6, 2 had 7 (W. Thomson, *Depths of the Sea*, p. 448); Eocene, and present time at great depths; *Mesocrinus* H. Carp., Cretaceous; *Bathocrinus* W. Thoms. (Fig. 206) recent at great depths, 10 arms, orals aborted.

Rhizocrinus (Fig. 207) was discovered by G. O. Sars among the Lofoten Islands in 1864. The interest of this discovery led to the expedition of H.M.S. *Lightning* in 1868, of the *Porcupine* 1869-70, when *Bathocrinus* was discovered, and later of the *Challenger* in 1874.

Fam. 4. **Saccocomidae.** Calyx small, hemispherical, non-pedunculate. 5 thin radials, elevated into ridges. Arms 5×2 , arm plates cylindrical with wing-like expansions, Upper Jurassic. *Saccocoma* Ag.

Fam. 5. **Pentacrinidae.** Calyx small, consisting of 5 basals, 5 radials,

and $5 \times 2-3$ primibrachials (with 5 small infrabasals in *Extracrinus*). Arms divided 1-10 times, with pinnules. Calyx cover membranous, containing thin loose plates. Without orals in adult. Stalk long, pentagonal, rarely cylindrical, with whorls of cirri, without root-like processes; two joints are united by syzygy at each node, of which the upper bears the cirri. Triassic to present time. *Pentacrinus* Miller (*Isocrinus* v. Meyer 1837) (Fig. 208), the 2nd primibrachial is axillary. Triassic to present time, *P. asterius* L. (*caput medusae* Mill.), Caribb. Sea, 120 fms.; *P. mülleri* Oerst, W. Indies 50-531 fms.; *P. wyville-thomsoni* Jeffreys, 800-1,100 fms. *Extracrinus* Austin (*Pentacrinus* Blum. 1837,) f. *Metacrinus* P. H. Carp., recent, Pacific. *Balanocrinus* Ag., f. *Dadocrinus* v. Meyer, Trias.

Fam. 6. **Comatulidae**. In the young state stalked, later unstalked and freewimming. Calyx composed of a centrodorsal plate with cirri; infrabasals visible only in larva, fused with centrodorsal (top stem-segment) in adult; 5 more or less reduced basals, which may be visible externally or hidden, 5 radials, and 5×2 or more primibrachs. Interradials absent. Calyx-cover membranous, rarely with thin plates. Orals absent in adult. Arms simple or branched, with pinnules, brachials alternate. More than 150 living species, mostly in shallow water. Lias to present time. *Antedon* Frémink. (*Comatula* Lmk. etc.) (Fig. 188). Arms fork once or more, the second primibrach axillary, Lias to present time; *Eudiocrinus* P. H. Carpenter, 5 undivided arms, f. and r. Pacific and Bay of Biscay, 50-900 fms. *Actinometra* Müller, mouth excentric, Jura to present time, most seas, littoral to 800 fms. *Atelecrinus* P. H. Carp., with basals visible on outside of calyx, r, trop. Atl. and Pac. *Promachocrinus* P. H. Carp., with 10 radials (basals 5), recent. Pacific and S. Sea, 70 to 1,800 fms. *Thiolliericrinus* Etallon, Jura and Chalk.

The position of *Thaumatoocrinus* P. H. Carpenter (one specimen only, S. Sea, 1,800 fathoms) is very uncertain. It is unstalked, has a calyx composed of a centrodorsal with cirri, 5 basals, 5 radials and 5 interrads which touch the basals, the anal interrads carries a tapering 4-jointed process; 5 arms, unbranched with pinnules; mouth central with 5 large orals separated from the edge of the calyx by 2 or 3 rows of small irregular plates. In the separation of its radials laterally by interrads it recalls the Cameraté family Rhodocrinidae. In *Reteocrinus* and *Xenocrinus*, of the same order, the radials are separated by a number of small interrads. In some recent Crinoids interrads are present but always above the radials; they are therefore interprimibrachs, etc. In the structure of its calyx and in the entire freedom of its arms, it resembles the Larviformia.

The following families may be mentioned here, though where they should be really placed in the system is a difficult question.

Fam. **Eugeniocrinidae**. Calyx composed of 5 (rarely 4) thick, firmly connected radials; basals are absent and the calyx cover is not known. Stalk short, composed of long, cylindrical broad joints, without cirri. Axial canals are present, and the basals are probably covered by the radials. Lias, Jurassic and lower Cretaceous of Europe. *Eugeniocrinus* Miller, *Eudesicrinus* Lorient, *Tetracrinus* Münster, *Phyllocrinus* d'Orb.

Fam. **Plicatoocrinidae**. Calyx composed of 4, 6, or 8 (rarely 5 or 7) high, thin radials and of a 4- to 6-sided undivided base. Cavity of cup wide and deep. Calyx cover unknown. The radials carry an axillary primibrach from which 2 unbranched arms arise. Stalk thin with long, cylindrical joints. *Plicatoocrinus* Münster. Upper Jurassic.

Fam. **Hyocrinidae**. Calyx high, composed of 3 basals, sometimes fused, and 5 radials nearly equal in length. Each radial bears a small undivided arm, brachials united by syzygy into groups of 2 or 3, only the distal of which bear pinnules. The proximal pinnules are longer than the distal and reach to the end of the arms. Calyx cover plated, with 5 large orals round the mouth, with covering plates. Water pores perforating the orals as in *Rhizocrinus*, but more numerous. *Hyocrinus* W. Thoms. (Fig. 209), 1,600 to 1,900 fms., Atlantic. By its calyx *Hyocrinus* is related to the *Larviformia*, and by its pinnules which all terminate at about the same level, the proximal being

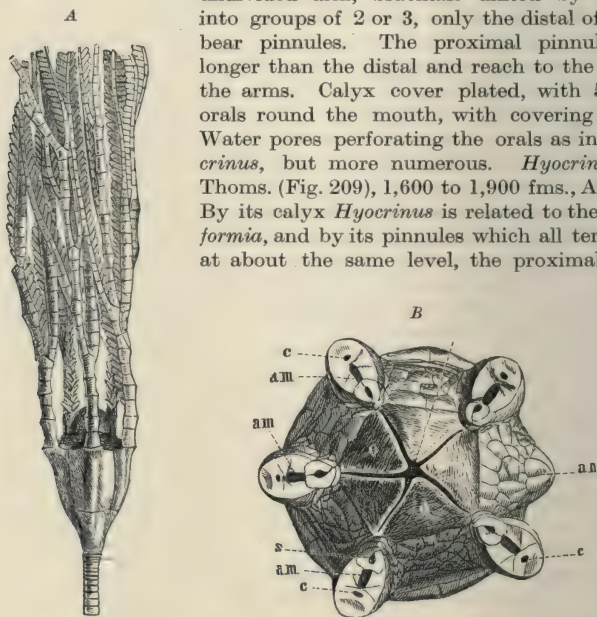


FIG. 209.—*Hyocrinus bethellianus* W. Thoms. (from Zittel, after W. Thoms.). A side-view, twice nat. size. B calyx-cover magnified; am ambulacral grooves of arms, c axial canal of arm joints, an anus, m mouth, o oral plates.

longer than the distal, to *Cyathocrinus*, where, however, we have to do with branching arms, not pinnules. *Gephyrocrinus* * Koehler and Bather, 1786 metres, Canaries.



FIG. 210.—*Holopus rangi* d'Orb. Side view, showing the 10 arms bent over the calyx cover (after Agassiz from Delage and Hérouard).

Fam. **Holopidae**. Calyx cup-shaped, containing all the viscera and fixed by its base to the substratum; no stalk. The calyx shows no distinct sutures dividing it into areas, so that it is impossible to say of what plates it is composed, though there are slight indications of a composition of radials at the upper end of cup. 10 massive arms closely rolled in upon the calyx cover (Fig. 210). Calyx cover with 5 large orals and marginal plates. Anus not observed. There is one primibrachial (if we may so call it) articulated to the edge of the cup and 10 arms-branches. Pinnules present. *Holopus* d'Orb. Deep water, Caribbean Sea. The first specimen found in 1857 was tetraradiate; more specimens subsequently came to hand, and it was eventually found by the *Blake*. The *Blake* specimens were dredged at 100 fms.

* *Mem. Soc. Zool. France*, 15, 1902, p. 68.

Cyathidium Steenstr., Cretaceous and Tertiary; *Cotylederma* Quenst., Lias.

Holopus is quite unlike any other Crinoid and it is impossible to fix the systematic position.* We do not even know the constitution of the calyx or the position of the anus. If the calyx is composed of basals and radials only, the genus ought to be placed with the Larviformia.

CYSTIDEA AND BLASTOIDEA.

The Cystids and Blastoids are entirely extinct and their fossils have only been found in the Palaeozoic rocks. They differ so much from living Echinoderms that it is by no means easy to interpret their structural features or to assign them to their proper systematic position. It has been customary with zoologists in recent years to associate them with the Crinoids in a subphylum **Pelmatozoa**, the remaining Echinoderm classes being united in a second subphylum which has been called **Eleutherozoa** (Bell) or **Echinozoa** (P. H. Carpenter). We cannot think that it is for the advantage of Zoology to adopt this classification. In the first place the Crinoids are not sufficiently distinct from other living Echinoderms to justify their assignment to a separate group of the dignity of a subphylum. In the second place our knowledge of Crinoid anatomy is detailed and complete, and based upon a minute study of living forms, while our knowledge of Cystids and Blastoids is vague and unsatisfactory to an exasperating degree. To take the forms assigned to the Cystidea alone, we cannot even be certain whether we are dealing with a single class or whether the range of structure met with would not more properly be distributed over several classes equal in value to the other Echinoderm classes. To the zoologist the great interest attaching to the study of Cystids consists in obtaining an answer to these questions. Their association with Crinoids seem to us to make it more difficult to obtain an answer. It places us in an entirely false position with regard to them, for it implies that we have a considerable knowledge of their anatomy and so may cause us, in the light of our complete knowledge of Crinoids, to strain our interpretation of difficult or doubtful Cystidean structures in a manner and to an extent which may lead us far from the truth. For these reasons

* It is placed by Jaekel and Bather near the Eugeniaerinae on account of its arm structure.

we prefer to subordinate the Cystidea and Blastoidea to no section of the Echinodermata and to treat them as independent classes, which in respect of their upturned mouth, their orally placed anus, and their aboral peduncle of attachment recall Crinoids, but which in other features of their anatomy show considerable diversity, some having obvious leanings towards Echinoids and Asteroids, and some seeming to be representative of a stage of structure in which the symmetry of the modern Echinoderm had not been evolved. It is indeed highly probable that the Cystids as at present constituted contain heterogeneous elements, which should be assigned to more than one independent class. Already highly competent authorities have separated from them the Edrioasteroidea* and there is much to be said for separating other members of the class.

Class CYSTIDEA.†

Stalked or unstalked forms with calyx which is usually composed of irregularly arranged plates. Arms are imperfectly developed or absent, and the radiate symmetry is often very imperfect or absent. The plates of the calyx usually possess pores.

The Cystidea are entirely extinct and only known to us by their fossil remains, which so far as our present information goes are confined to the Palaeozoic rocks. For this reason their structure is and must remain very imperfectly known, and the class presents great difficulties to the zoologist. These cannot be overcome and we must content ourselves in this

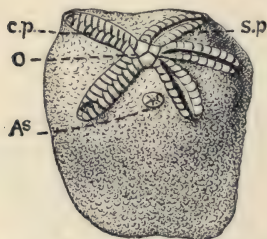


FIG. 211.—*Cystaster granulatus* from the posterior side showing the oral surface in perspective. The two left-hand rays retain the covering plates which are absent from the others (from Bather) $\times 3$. *As* anus; *cp* covering plates; *o* peristomial plates; *sp* side plates.

work with the description of a few forms which seem to represent the considerable range of structure found in the group. For fuller information we refer the reader to the excellent account contained in the two works cited.

The most significant characters of the Cystids are (1) the irregularity in the arrangement of the thecal plates which is so often found in them; (2) the absence or feeble development of arm-like structures; (3) the fact that the generative organ seems usually to have been single and not radially arranged; (4) the fact that in some of them there does not appear to have been a radial symmetry. If we are to have phylogenetic speculations these characters must obviously be taken into very careful consideration.

* See Bather, *op. cit.*

† Zittel's *Text-Book of Palaeontology*, vol. 1, London, MacMillan & Co., 1900. F. A. Bather, chapter on *Pelmatozoa* in Lankester's *Treatise on Zoology*, London, A. and C. Black, 1900. O. Jaekel, *Stammesgeschichte der Pelmatozoen*, Berlin, 1899.

The body consists of a calyx which is either prolonged aborally into a stalk (Fig. 215, etc.) or is without a stalk (Fig. 211, etc.) In the latter case the body was probably attached by its aboral surface to the substratum. When a stalk is present it frequently has rather the appearance of a tapering aboral continuation of the body (Fig. 212) than of a sharply differentiated stem like that of the stalked Crinoids. The stem, which is often very short and without cirri or roots, does not, as a rule, appear to have served for attachment. It is frequently coiled. The calcareous plates of the body wall are usually numerous and irregularly arranged; but sometimes they are larger, few in number and arranged in definite cycles (e.g. *Cystoblastus* Fig. 213). They are united by sutures. There is as a rule no sharp line of demarcation between the oral and aboral surfaces, or between the plates of the radial and interradial areas.

The mouth is at or near the centre of the oral surface and is sometimes covered by oral plates. In the simplest forms ambulacral grooves are not visible (Figs. 212, 214) and no radial structure can be made out, but it is asserted by Barrande that such forms probably have subtegmina grooves. Usually ambulacral grooves are present, and they are placed either on the surface of the calyx (Fig. 217) or on processes of the edge of the mouth (Fig. 216). They vary in number from two to five and may branch. They frequently possess covering plates (Fig. 219) which in life must have been capable of being folded back so as to expose the groove. Arms are often quite absent, and when present are usually small. They either project from the edge of the mouth (Fig. 216) or further out from the calyx (Fig. 220). The arms vary in number from two to thirteen. In some cases the so-called arms resemble pinnules, as in *Glyptosphaera*, *Protocrinus* (Fig. 217) in which the ambulacral grooves branch and end in small arms: these may perhaps be called **brachioles**, though it is often impossible to settle whether to apply the term brachiole or pinnule to an arm-like process. Undoubted pinnules arise from the edges of the ambulacral grooves in some cases and the ambulacral grooves are continued on to them (Fig. 215). The anus is on the same surface as the mouth but excentrically placed in an interradius (Figs. 211, 217, etc.) Between it and the mouth two openings can in some cases be made out: one of these, that nearest the anus, is interpreted as the genital opening; the other is supposed to be the water-pore (Fig. 214). If the interpretation of the first of these openings is correct, it would appear that the genital organ of Cystids is in the calyx and is not radially

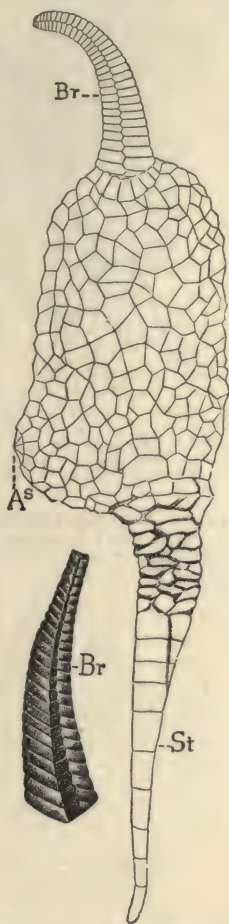


FIG. 212. — *Dendrocystis Sedgwicki* (after Barrande from Bather). *As* anus *Br* the arm-like appendage; *st* stem.

arranged. But the so-called genital opening has only been observed in a few cases, and it may be that in the forms with pinnules the gonads were in them. The identification of the other opening is too precarious to

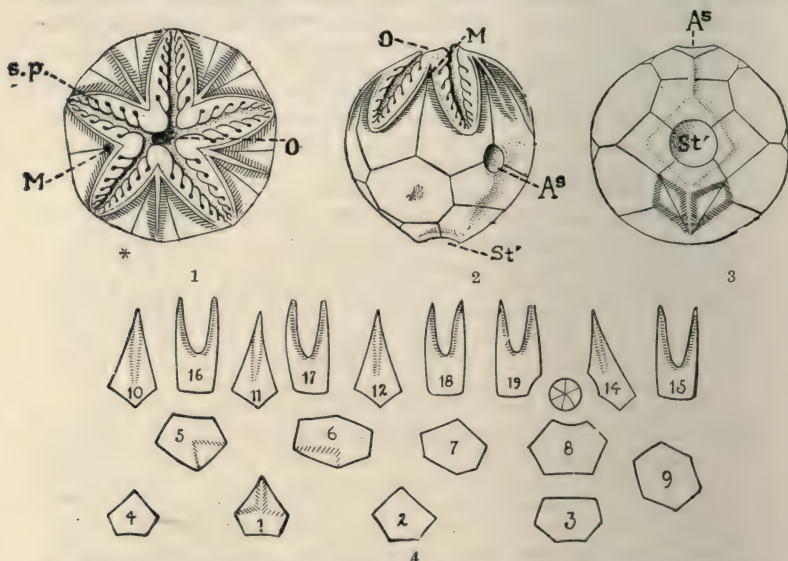


FIG. 213.—*Cystoblastus Leuchtenbergi* (after Volborth, from Bather). 1 oral; 2 posterior; 3 aboral view; 4 analysis, with plates numbered. A^s anus; * anal interradius in 1; M water-pore or generative opening; sp plates on the floor of the arm grooves; St' attachment of stem.

allow of our drawing any inference as to the relative position of the water-pore and anus, but when the madreporite can undoubtedly be distinguished, it is placed in the same interradius as the anus.

The calcareous plates of Cystids often seem to be composed of three distinct layers: a smooth and thin outer layer, the *epistereom*; a thick

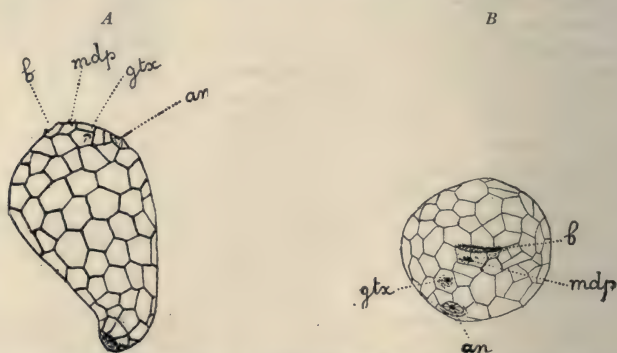


FIG. 214.—*Aristocystis bohemicus*. A, from the left side, B from the oral face (after Barande). an anus; b mouth; gtx generative opening; mdp hydropore.

middle layer traversed by canals, the *mesostereom*; and a thin smooth inner layer, the *hypostereom*. In many Cystidea the middle layer is traversed at right angles to the surface by canals, the ends of which are closed by the epistereom and hypostereom, if these layers are preserved. If the latter are weathered off the canals appear to open in surface pores.

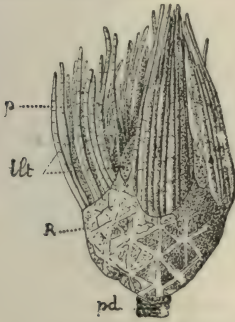


FIG. 215. — *Asteroblastus Volborthi* (after Schmidt and Bather, from Delage and Hérouard). *olt* oral plates; *p* pinnules; *pd* stalk; *R* radial plates.

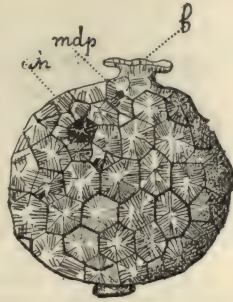


FIG. 216. — *Echinospaera aurantium* (after Volborth). *an* anus; *b* mouth; *mdp* water-pore. The stalk projects below.

These pores may occur singly (*haplopores*) or in pairs (*diplopores*). When the canals are in pairs, the external openings of a pair are placed in a common pit on the stereom.

In some forms, classed as Rhombifera, canals are found in the mesostereom traversing the plates parallel to the surface; these canals extend across the suture, at right angles to it, to be continuous with similarly arranged canals on the neighbouring plates (Fig. 218). They are so arranged that their terminations form a rhombic figure, the diagonal of which is occupied by the suture between the plates concerned. For this reason and because the terminations of the canals often bend outwards and appear on the surface as pores, the figures caused by them are called *pore-rhombs* (Fig. 218). At their ends, and sometimes also near the suture, the canals may also bend or send a branch inwards to the inner surface of the mesostereom. Prof. Jaekel compares these terminal vertical canals with the two canals of a diplopore, and supposes the horizontal canal to represent the peri-poral depression greatly extended.

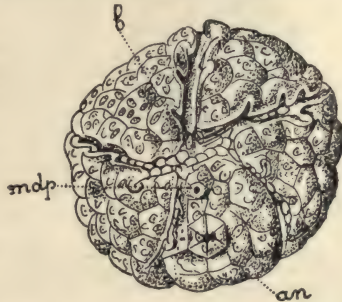


FIG. 217. — *Protocrinus oviformis* (after Volborth from Delage and Hérouard). *an* anus; *b* mouth; *mdp* water-pore.

In some forms, however, the canals of the rhombs have the form of grooves, the sides of which project on the external surface of the plates, so that the stereom appears as though thrown into folds. *Pectini-rhombs* are pore-rhombs in which such folds or grooves are very deep and at the

same time restricted in area, and often surrounded by a raised rim. While normal pore-rhombs are usually found on all or most of the plates, pectini-rhombs only occur on a few plates (Fig. 219) in definite positions. The grooves of a pectini-rhomb are frequently filled up or bridged over near the suture, so that the rhomb as seen from outside appears to consist of isolated halves. These halves, however, remain connected within the mesostereom.



FIG. 218.—Pore-rhombs (a) of *Echinospaera*, (b) of *Caryocrinus* (magnified, from Zittel). The left half of a is abraded, so that the canals appear as open grooves.

It appears that the canals, whether of the ordinary pores or of the pore-rhombs are typically in the mesostereom, and do not open on the surface, being covered by the epistereom and hypostereom respectively, though if these layers are absent through weathering or other cause, the canals appear in some cases to be open. It is possible that they are due to tracts of stroma containing blood spaces traversing the stereom, and Mr. Bather has suggested that the canals of the pore-rhombs are develop-

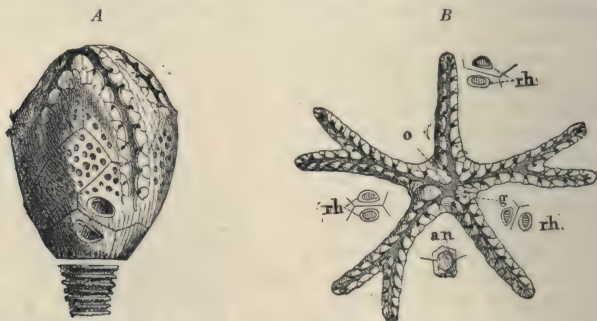


FIG. 219.—*Callocystites Jewetti* Hall. Upper Silurian, Lockport, New York. A from the side (natural size). B ambulacral grooves and two pectinated rhombs *rh*. *an* anus; *o* genital opening; *o* mouth.

ments from foldings of the mesostereom, such as exist in many Crinoids, being due to the natural tension of the stroma fibres in the integument as it becomes calcified. These foldings are covered towards the surface by the secondary deposition of epistereom and hypostereom. When the epistereom was very thin or absent, as appears sometimes to have been the case, or when it has been removed by weathering, these grooves of the mesostereom appear to be open and their edges project on the surface of the plates as ridges. Whether this view of the real nature of the canals is

correct or not, it appears certain that they could not have been tubes leading from the exterior into the body-cavity of the animal, because they are in so many cases closed by the layers of epi- and hypostereom above referred to. Structures very similar to pore-rhombs, having the form of deep folds crossing the sutures between the plates are found in many fossil Crinoids (see especially *Porocrinus*, *Carabocrinus* and *Hybocrinus*). The ordinary structure of the mesostereom, simulating folds, is best seen in genera with large plates such as *Marsupites* and *Crotalocrinus*.

In no Cystid except the Edrioasterida are pores present along the ambulacral grooves which can have served for the passage of tube-feet. Whether tube-feet were present is, however, another question.

The Cystids make their appearance in the Cambrian in which and in the Silurian they are represented by a great diversity of forms. They die out in the Permian.

Order 1. AMPHORIDA.

Forms without radial symmetry. Often with irregular arrangement of thecal plates; usually with a stalk. Body often bilaterally compressed with two food-grooves (*Trochocystis*). The plates may possess canals, but their ends are not open. A variable number of arm-like processes may be present in some genera. *Aristocystis* Bar. (Fig. 214), upper Cambrian. *Dendrocystis* Bar. (Fig. 212), U. Cambrian.

Order 2. RHOMBIFERA.

Usually with a stalk. With radial symmetry of the ambulacral grooves and in some forms of the thecal plates. The ambulacral grooves usually extend on to processes of the theca (brachioles, arms) arising at the edge of the mouth (exothecal) (Fig. 216) or they may extend outwards for a certain distance on the theca, but in this case also they are exothecal as they do not lie on the thecal plates, but on special plates. With pore-rhombs. When the plates are large and regular they are arranged in cycles and the base is dicyclic, i.e. infrabasals, basals, and radials are present. In *Caryocrinus* and *Hemicosmites* there are 6 basals and 6 radials, in most others 5. *Echinospaera* Wahl. (Fig. 216), arms unknown, U. Cambrian. *Arachnocystis* Neum., usually three arms, U. Cambrian. *Cystoblastus* Volb. (Fig. 213), U. Cambrian, may possibly have possessed pinnules arising from the edges of the ambulacral grooves, with 4 infrabasals, 5 basals and 5 radials. *Pleurocystis* Bill, U. Cambrian, with two arms. *Callocystites* Hall (Fig. 219), Silurian, with 4 pectinated rhombs, with ambulacral grooves on the calyx, some of which bifurcate. *Echinoencrinus* H. v. Mayer, 3 small arms, U. Cambrian. *Lepadocrinus* Conrad, Silurian. *Caryocrinus* Say, arms 6-13 in number, Silurian (Fig. 218). *Hemicosmites* v. Buch, U. Cambrian.

Order 3. DIPLOPORIDA.

With radial symmetry; with ambulacral grooves on the theca (epithecal, Fig. 221), provided with lateral pinnules (Fig. 215), and continued on to terminal brachioles (Fig. 220); with diplopores, without rhombs. *Eucystis* Ang. (Fig. 220), U. Cambrian. *Protocrinus* Eich. (Fig. 217), U. Cambrian. *Mesocystis* Bather (*Mesites* Hoff.), U. Cambrian, with 5 ambulacra with covering plates



FIG. 220.—*Eucystis variopunctata* (after Angelin, from Delage and Hérourard). An anus.

and probably with pinnules attached to the covering plates; the pinnules distinguish them from Echinoids which they otherwise resemble (Fig. 221). The ambulacral grooves extend almost to the aboral pole, and there are furrows passing between the covering plates which may have served for tube-feet; they do not appear to have had a stalk but they may have been fixed by the aboral pole. *Asteroblastus* Eichw. (Fig. 215), U. Cambrian. *Blastoidocrinus* Billings, U. Cambrian. The two last named genera are placed by Bather with the Blastoids.

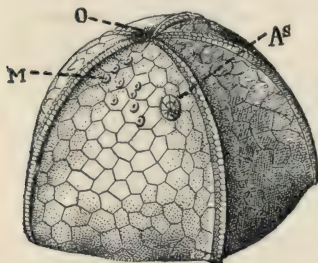


FIG. 221.—*Mesocystis Pusirefskii* (restored after Hoffmann and Nitikin, from Bather). *As* anus; *M* water-pores or perforations caused by a parasite; *O* mouth.

Order 4. EDRIOASTERIDA.

With radial symmetry and, in some forms, pores between the ambulacral plates as though for the passage of tube-feet; the theca is composed of irregular plates, the madreporite is well marked and lies near the mouth in the same interradius as the anus (Fig. 222); no pinnules. There does not appear to have been a stalk, though in some cases they may have adhered by the aboral surface. They present some resemblances to Asteroids. U. Cambrian to Carboniferous. *Cystaster* Hall (Fig. 211), U. Cambrian. *Edrioaster* Bell., U. Cambrian (Fig. 222). *Agelacrinus* Vanuxem, U. Cambrian, Silurian, Devonian, Carboniferous.

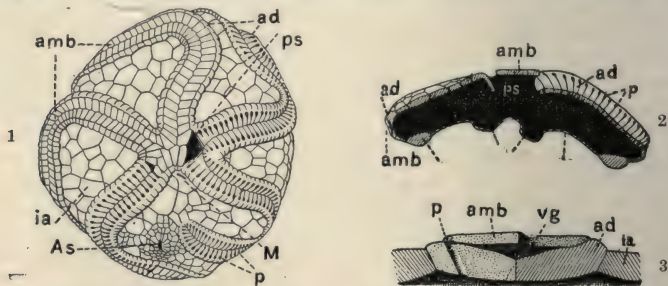


FIG. 222.—*Edrioaster Bigsbyi* (after Bather). 1 oral view. 2 section through a radius and interradius of the same specimen. 3 Section across an ambulacrum. *ad* flooring plates of the ambulacral grooves; *amb* covering plates of grooves; *As* anus; *ia* interambulacral plates; *M* madreporite; *p* pores between the ambulacral plates; *ps* peristome with covering plates; *vg* ventral groove.

Class BLASTOIDEA.*

Pentamerous forms without arms, with radial ambulacra bearing pinnules, with a well-plated monocyclic calyx, with hydrospires, without pores.

The Blastoids are entirely extinct, being confined to the Palaeozoic

* Etheridge and Carpenter, *Catalogue of the Blastoidea in the Geological Department of the British Museum*, 1886. Bather, *op. cit.*; Zittel, *op. cit.*

period. They make their appearance in the Silurian, and reach their richest development in the Carboniferous. As at present constituted the class is a well defined one.* They approach the Cystids through the Diploporida. The calyx is somewhat ovoid and either has a short stalk



FIG. 223.—Analysis of calyx of *Pentremites florealis* (from Zittel). Aboral view, the posterior deltoide is downwards in the figure. *b* basals; *r* radials; *ir* deltoids (interradial).

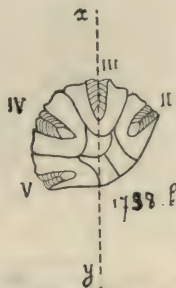


FIG. 224.—Apical region of *Eleutheroocrinus Cassedayi* (after Etheridge and Carpenter). *α γ* axis passing through the anal interradius and the opposite radius (III); II-V four of the radii.

or is without a stalk. It consists of three rows of plates (Fig. 223); three basals, two of which are larger than the third as though composed of two pieces fused; five radials (*r*) each of which is forked at its radial end; and five interradial *deltoids* (*ir*), which surround the peristome. The spaces between the forks of the radials and between the deltoids are

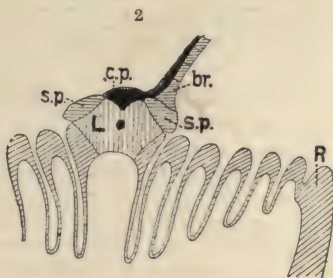
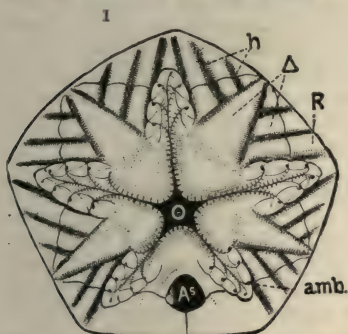


FIG. 225.—*Codaster trilobatus* (after Bather). 1 oral surface of young form $\times 6$. 2 slightly restored section through a radius. In 1 the central parts of the deltoids are prominent. *amb* ambulacrum; *As* anus; *br* pinnule (brachiole); *c.p.* covering plates of ambulacral groove; *h* hydrospsire slits; the hydrospsires of the anal interradius are imperfect in this genus; *L* lancet plate, containing canal; *O* mouth; *R* radial; *s.p.* side plate; Δ deltoide.

occupied by the ambulacra (Fig. 225 *amb*). The ambulacra are petaloid and are traversed by a median ambulacral groove. The floor of this

* Bather has established a subclass of Blastoids to which he applies the name Protoblastoidea to include *Asteroblastus* and *Blastoidocrinus* (p. 310). These genera, however, are without hydrospsires and possess diplopores.

groove is formed by a median plate called the *lancet plate* (Fig. 225, 2, *L*) and on each side by lateral plates (*sp*). The lancet-plate contains a canal (Fig. 225) which in the neighbourhood of the mouth opens into the cavity of the calyx. The ambulacral groove possesses covering plates (*c.p*) which can only be discerned in a few specimens and which are continued over the mouth. Crossing, at right angles, the sutures between the radials and deltoids, are some deep slits (Fig. 225 *h*) which lead into pouches projecting into the calyx-cavity (Fig. 225, 2). These pouches are the **hydrospires**; they are disposed parallel to the ambulacral grooves (Fig. 225). Pinnules or brachioles (*br*) are attached to the side plates and furrows pass from the ambulacral groove across the exposed part of the lancet plate on to them. When preserved, they are usually folded over the grooves. There is no evidence for the existence of tube-feet. The anus is in an interradius at the junction of a deltoid with two radials (*As*). It is not in the interradius of the small basal. The arrangement of the hydrospires described above is that found in

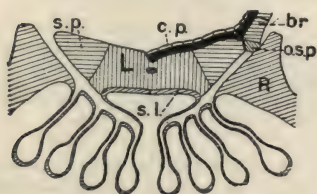


FIG. 226.—Section across a radius of *Pentremites* (after Bather). *br* pinnule (brachiole); *c.p* covering plate; *o.s.p* outer side-plate; *R* radial; *s.l* sub-lancet plate (in many genera a sub-lancet plate is found beneath the lancet plate); *s.p* side plate. The hydrospires here open into a canal beneath the side plates and lancet plate called the hydrospire canal.

Codaster; in other Blastoids it is slightly different. They are usually arranged more compactly and their openings become covered over by extensions outwards of the lancet plate and the side plates of the ambulacral groove (Fig. 226). A canal—the hydrospire canal—is thus formed. It opens to the exterior by a series of apertures between the side plates on each side of the lancet plate, called the **hydrospires**, and by a larger opening near the mouth between the deltoid, the proximal side-plate and the lancet plate; these openings are called the **spiracles**. They are ten in number, but frequently they become united in pairs, one joining with that of the adjacent radius, so

that there are five only. The spiracles adjoining the anus are often confluent with it.

In some genera (*Astrocrinus* and *Eleutheroocrinus*) one of the ambulacra is different from the rest. The meaning of the hydrospires is quite unknown. They have been compared to the genital bursae of Ophiurids and supposed to have been respiratory in function. They have also been compared with the canals of the pore-rhombs of Cystids. Their relation to the sutures between the deltoids and radials which is so clearly seen in *Codaster* no doubt suggests this comparison, and if there is anything in the suggestion on p. 308 that the canals of the pore-rhombs are due to foldings of the stereom, there may be something in it.

In the general form of their body the Blastoids present a certain resemblance to Echinoids, but they differ from these in the fact that they are usually stalked, in the presence of pinnules, and in the composition of the calyx. The principal genera are: *Pentremites* Say (Fig. 227), Devonian and Carboniferous. *Mesoblastus* E. and C., Carboniferous. *Troostocrinus* Shum., Silurian. *Tricoelocrinus* M. and W., Carboniferous (Fig. 227). *Nucleocrinus* Conrad (*Elaeocrinus* Roemer), Devonian. *Orbitremites* Austin (*Granatocrinus* Hall), Carboniferous (Fig. 227). *Hetero-*

blastus E. and C., Carboniferous Limestone. *Codaster* McCoy, Silurian to Carboniferous. *Phaenochisma* E. and C., Devonian, Carboniferous. *Orophocrinus* v. Seebach, Carboniferous. *Eleutheroocrinus* Shum. and Yand., Devonian. *Astrocrinus* Austin, Carboniferous Limestone.

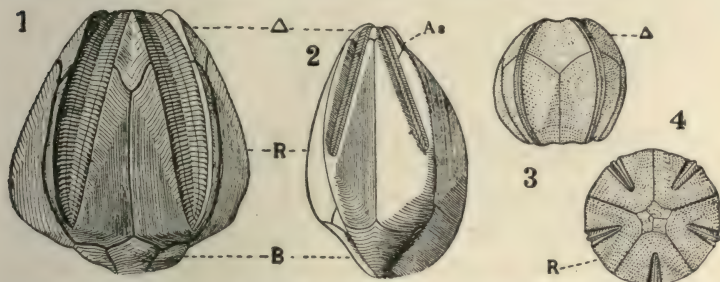


FIG. 227.—Thecas of typical Blastoids (after Bather). 1 *Pentremites robustus*. 2 *Tricoelocrinus woodmani*. 3 and 4 *Orbitremites* (*Granatocrinus*) *orbicularis* from the side and from below. All nat. size.



CHAPTER IV.

PHYLUM ARTHROPODA.*

Segmented animals generally with a firm external skeleton, jointed appendages, and foot-jaws. The general disposition of the chief organs is the same as in Annelids, but the coelom, though present and discharging important functions, does not develop a perivisceral portion. The perivisceral cavity consists entirely of blood-sinuses.

THE relationship of the Arthropoda to the Annelida has led to their classification in one group, the *Annulosa* of M'Leay.

* The literature on the Arthropoda is referred to under the headings of the several groups. There are however two topics dealt with in this section, to the literature of which it may be convenient to the reader to have his attention drawn.

On the segmentation of the Arthropod head and other cognate questions see :—

K. Kishinouye, Note on the coelomic cavity of the spider, *Journ. Coll. Sc. Tokyo*, vol. vi. (1894), p. 287. E. S. Goodrich, The relation of the Arthropod Head to the Annelid Prostomium (*Q.J.M.S.*, vol. 40, 1898, p. 247). E. R. Lankester, The structure and classification of the Arthropoda, *Q.J.M.S.*, vol. 47 (1904), p. 523, reprinted from the *Encyclopaedia Britannica*, Tenth Ed., New Volume I. 1902, Article Arthropoda. R. Heymons, Die Entwicklungsgeschichte der Scolopender, *Zoologica*, Heft 13 (1901). Essays by G. H. Carpenter on the relationships between the classes of the Arthropoda, *Proc. R. Irish Academy*, vol. 24 B. (1902-4), p. 320 (in which a bibliography of much recent work bearing on the matter will be found) and Segmentation and Phylogeny of the Arthropoda, with an account of the maxillae of *Polyxenus*, *Q.J.M.S.*, vol. 49 (1905-6), p. 469. Sedgwick A., A monograph on the development of *Peripatus capensis*, *Q.J.M.S.*, vols. 25-28 (1885-8).

On the Eyes of Arthropods see :—

Lankester and Bourne, The minute structure of the lateral and central eyes of *Scorpio* and *Limulus*, *Q.J.M.S.*, 1883, p. 177. Watase, S., On the morphology of the compound eyes of Arthropods, *Studies from the Biological Laboratories, Johns Hopkins University*, iv (1889), p. 287. Kishinouye, K., On the development of Araneina, *Journ. Coll. Sc. Imp. Univ. Tokyo*, vol. 4, pt. 1, 1891. Grenacher, H., *Unt. über das Sehorgan d. Arthropoden*, Göttingen, 1879. Exner, Sig., *Die Physiologie der facettirten Augen von Krebsen u. Insecten*, Leipzig u. Wien, 1891. Chun, Atlantis, *Zoologica*, Bd. vii. Heft. 19 (1896). Parker G. H., The retina and optic ganglia in Arthropods, *Mitth. aus d. zool. Stat. zu Neapel*, Bd. xii, 1897, p. 1. Szczawinska, W., Contrib. à l'étude d. yeux de quelques crustacées . . *Arch. Biol.*, T. 10, p. 523.

It is displayed in the metameric segmentation of the body, the lateral extension of the segments into processes which subserve locomotion, the presence of a ventral nerve cord surrounding the oesophagus anteriorly and of a dorsal heart. We may therefore begin our review of the characters of the Arthropoda as a whole by drawing a comparison between them and the Annelida.

In the Annelida the body is covered by a soft and chitinous covering. The mouth opens on the first segment of the body and a prestomial lobe projects in front of it on the dorsal side. Each segment contains, in the Polychaeta, a spacious coelomic cavity, that of the first extending forwards into the prestomium.* The supraoesophageal ganglion lies in the prestomial lobe, and the first member of the ventral ganglionic chain behind the mouth in the first segment (peristomial region). The prestomium bears a pair of tentacular appendages (sometimes with a median tentacle in addition), and the parapodia which project at the sides of the body, although differentiated for locomotory and tactile functions, are never jointed, and none of them are modified as jaws to assist the introduction of food into the mouth. The characteristic annelidan disposition of the nephridia and gonads has been fully treated in an earlier part of the present work and need not be here recapitulated.

The cuticle in the Arthropoda is more rigid than that of the Annelida and is generally hardened by a deposit of salts of lime. It is secreted by a layer of cells, the epi- or hypodermis, and from time to time during the period of growth of the animal the hard outer layers of the cuticle are separated from the inner layers, and ruptured, the animal emerging from its cast "skin" (ecdysis). The soft inner layers then expand to accommodate the growing body.

Except in some cases, and usually in the posterior region, the segments are produced laterally into limbs, and these, like the body from which they spring, are divided into segments by annular tracts of flexible cuticle intervening between the hard and allowing movement between the successive segments and of the whole limb upon the body.

Movement is effected by a muscular system, which is contained

* See, however, the remarks on this subject in the chapter on Annelida, vol. I, p. 448.

within the firm external cuticle, and the bands of it pass from point to point across the articulations. The Arthropoda are thus markedly contrasted with the Chordata, in which the skeletal structures are internal and covered by the muscles.* There is no contractile dermomyofascial body wall, except in *Peripatus*.

On the vastly increased mechanical possibilities afforded by such an exoskeleton, with its plates of varying degrees of rigidity and delicately adjusted systems of levers the active many-sided life of the Arthropoda depends. Associated with the increased powers of locomotion which such a skeleton confers we find a high development of the sense organs and nervous system, and, in Insects, the elaborate social instincts which have ever excited the wonder of mankind.

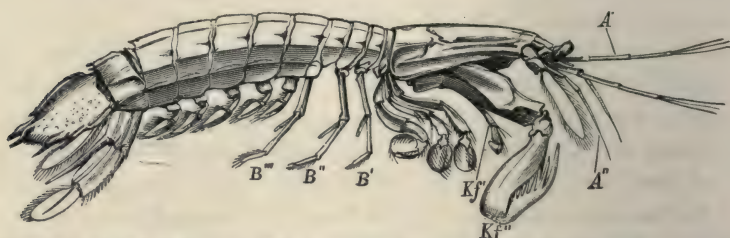


FIG. 228.—*Squilla mantis*. A', A'' first and second antennae; B', B'', B''' the three pairs of biramous appendages (6th–8th thoracic); Kf', Kf'' first and second maxillipeds (after Claus).

In no Arthropod is the body-cavity coelomic. It consists of blood-spaces, constituting a haemocoel. The development of members of the several groups however reveals the fact that a coelom exists, in a more or less modified form, in all.

In *Peripatus* the somites are formed from the mesoblastic bands as paired structures, a pair to each segment at the sides of the elongated blastopore (p. 570). They are hollow from their first appearance and the cavity which each contains is the coelomic cavity. From them are formed (a) the nephridia, a pair to each trunk segment, with their end-sacs; and (b) the tubular generative organs. The latter arise by the junction of the dorsal portions of the paired coelomic cavities of certain of the posterior segments, and their connexion with a posterior

* The fibro-cartilaginous endosternum of *Limulus* and other Arachnids is however comparable, as regards its relation to muscles, with the chordate skeleton.

pair of nephridia, which thus furnish the opening to the exterior. These ducts in the female retain a ciliated lining (Gaffron), the only known instance of the occurrence of a ciliated tract among the Arthropoda.

The other groups of Arthropods present various stages of modification of this primitive arrangement. In the Arachnida segmented coelomic sacks (somites) are formed, and in their walls the gonads are developed. In *Scorpio* five pairs of segmental ducts appear in the embryo (in segments 3-6 and in the 8th *). Some of these disappear in the adult, but those of the fifth persist, though with loss of the external aperture, as the coxal glands, and those of the eighth as the ducts of the gonads (Brauer). In other Arachnids a single pair of nephridia (corresponding to the fifth pair of appendages) also persists as the coxal glands.

In Myriapoda and Insects coelomic sacks are also developed and from the walls of some of these the gonads are formed, but, the excretory function having in these groups been in most cases taken over by diverticula of the alimentary canal, no trace of nephridia has been found.

In Crustacea two pairs of nephridia persist, though they are rarely found to coexist, as the antennal and shell glands, but the mesoblast presents in this group the extreme of differentiation from the annelidan arrangement, there being scarcely any traces of its segmentation or of general coelomic cavities. In all however the genital ducts are mesoblastic in origin and it is thus open to us to regard them as derived from a pair of nephridia, as analogy with *Peripatus* and *Scorpio* would suggest.

Connected with the presence of a haemocoelic body cavity in place of the coelomic body-cavity of Annelids is another characteristic feature of the Arthropoda, the relation of the heart to the pericardial sinus.

The heart in this group is a longitudinal dorsal vessel, perforated by one or more pairs of lateral ostia. These admit blood from the pericardium, a special compartment of the system of haemocoelic spaces which is separated from the rest by a horizontal septum lying beneath it.

* Counting, with Brauer, the cheliceral segment as the first. It is however counted as the second (cf. p. 323) in the table on p. 525.

In Arthropods one or more of the anterior appendages is modified to form jaws (foot-jaws), and in association with this we find a concentration and fusion of some of the anterior segments of the body by which they form a group distinct from the segments behind and constitute a *head*.

From the study of development it is clear that, as pointed out by Lankester, there occurs in Arthropods a shifting of the position of the mouth backwards, in relation to the segments of the head; so that it may come to lie in the adult on the ventral side of the segment which is apparently * the second, third or fourth. The first pair of appendages having the character of jaws lies either at the sides of or immediately behind the mouth, and hence in the several groups the jaws are the appendages of the apparent second, third or fourth segment, the appendages anterior to them taking on other and generally tactile functions or in some cases disappearing altogether. Bearing in mind the fact that in *Peripatus* the blastopore extends, at one stage in development, as a fissure along the ventral median line between mouth and anus, it may without difficulty be conceived how such an alteration in the position of the mouth may have occurred.

The segmentation of the arthropod head. It would be interesting, if it were possible, to determine the relation between the anterior segments of the body which in the several divisions of Arthropods form the head and also between them and the anterior segments of the Annelida.

The post-cephalic segments are very variable in number in both groups. The body is divided up, here into a larger, there into a smaller number of segments, and the problem of the precise homology of a particular segment in one class with the numerically corresponding segment in another is probably without reality.

With regard to the head however the case appears to be different. Within the divisions of the Arthropoda (*Insecta*, *Crustacea*, etc.) the number of head-segments shows a remarkable constancy; the segmentation has become, as it were, numerically stereotyped, and we may inquire how far the segments correspond in the several divisions, and whether a numeri-

* The difficulty of determining which segment of an Arthropod corresponds with the first in the Annelida is pointed out below.

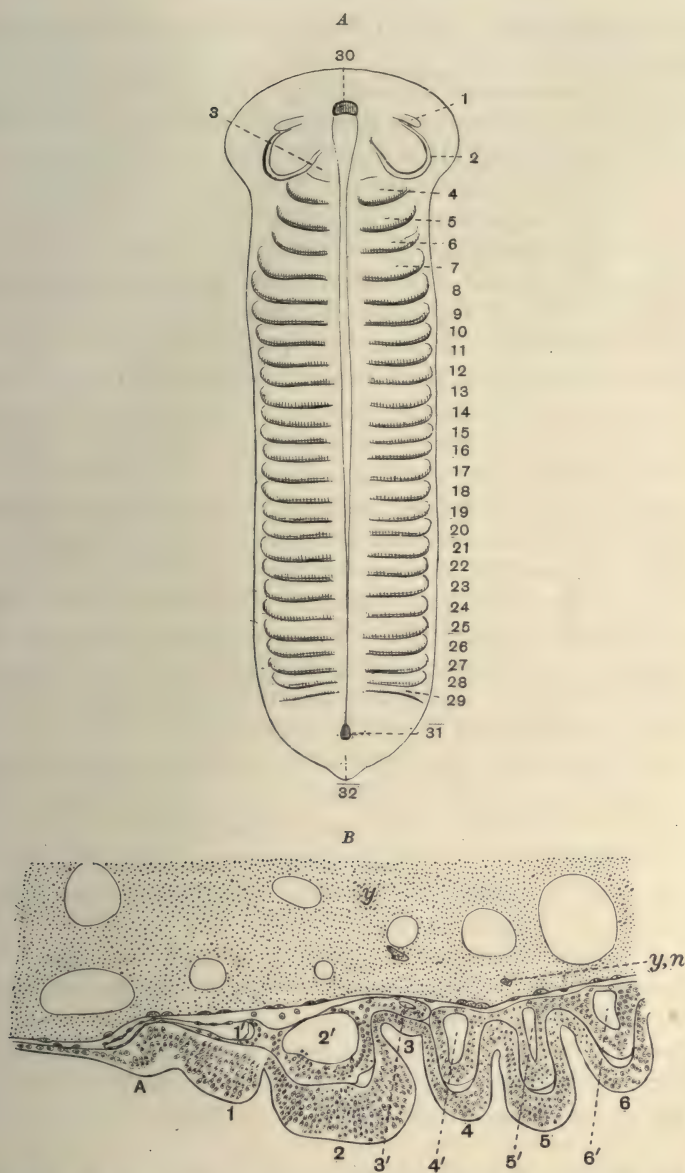


FIG. 229.—Blastoderm of *Scolopendra cingulata*; *A* ventral aspect. *B* Longitudinal section through a blastoderm at a somewhat later stage, on one side of the middle line. *A* Preoral region, lateral region of the acron; 1 pre-antenna; 2 antenna; 3 intercalated segment; 4 mandible; 5 first, and 6 second maxilla; 1'-6' the coelomic sacs corresponding to these appendages; 7-29 post-cephalic segments; 30 mouth; 31 anus; 32 telson; *y* yolk; *yn* yolk nuclei (after Heymons).

cal correspondence can be traced between Arthropoda and Annelida.

In the development of the head, as of the rest of the body, evidence of the existence of a segment is afforded by the formation in development (1) of a pair of mesoblastic somites, which may retain their coelomic cavities, (2) of a pair of ganglia (forming a neuromere) corresponding in position with the somite, and (3) of a pair of appendages.

Among the higher Arthropoda whose development is known to us, the Chilopod *Scolopendra* appears to present the simplest and most primitive condition of the segments of the body. It has been investigated by Heymons, and Figs. 229A and B are taken from his monograph. In front of the antennal segment and marked, like it and all the segments behind it, by a pair of coelomic sacks as well as by a neuromere, is a preantennal segment from which for a short time small tentacular preantennal appendages (1) project. Between antennae (2) and mandibles (4) a segment is formed, marked by neuromere and coelomic sacks but without appendages—the premandibular or as it has been called intercalated* segment (3). Then come the segments of the mandibles and of the two maxillae of *Scolopendra*. The twenty-three post-cephalic segments follow, the appendages of the first (7) being transformed into the poison claws.

The preantennae are formed at the sides of or a little behind the mouth, though the latter subsequently moves back and lies between the mandibles. In front of the mouth is formed (at a later stage than that figured) the labrum, projecting backwards from the clypeus; behind it the bilobed hypopharynx subsequently appears.

An unpaired median thickening of epiblast is formed from the clypeal region. It is called by Heymons the *archicerebrum*. Two paired pitted thickenings of the epiblast on either side of it are the medial and lateral brain rudiments of Heymons. From these five centres, one median and two paired, the *syncerebrum* of Heymons is formed.

* If the name "intercalar-segment" were to be taken literally, as meaning that a new segment existed in a given individual between two segments, which were adjacent in its parents, the designation of the segments by number would be at once recognized as inapplicable. We have however no very satisfactory grounds for asserting or denying the possibility of such an intercalation.

The two paired thickenings are so disposed that they continue on either side the line of the paired ganglia of the neuromeres belonging to the postoral part of the body, so that the arrangement raises the question whether we have not in these medial and lateral paired rudiments the representatives of segments anterior to the preantennal. This latter however is the first in relation with which coelomic sacs and appendages are formed, and we may, provisionally at least, reckon it, with Heymons, the first metamere.

With the complex syncerebrum the neuromere of the pre-antennal segment (the protocerebrum s. str. of Heymons *) becomes fused to form the dorsal lobes of the adult brain, the *procerebrum* of Heymons, from which the optic nerves arise, while the neuromere of the antennae forms the anterior paired lobes giving off the antennary nerves—the *mesocerebrum* or deutocerebrum. The neuromere of the premandibular ganglion forms the posterior and ventral pair of lobes—the *metacerebrum* or tritocerebrum, from which the commissures pass to the suboesophageal ganglion. The suboesophageal ganglion is formed by the union of three neuromeres, namely those of the mandibular and two maxillary segments of *Scolopendra*.

In the lower Insects (Apterygota, Orthoptera) the segments of the head are laid down in a very similar manner, but no trace has been found of the coelomic sacks or the appendages of the preantennary segment. The antennal segment is here the first to bear an appendage and to contain distinct mesoblastic sacks. The premandibular segment is also well developed, and in *Forficula* the nuclei of the mesoblastic somite belonging to it are arranged in two layers, though an actual cavity has not been recognized. The only cases in which appendages are known to be borne by this segment are those of the primitive Thysanuran genus *Campodea*, in which Hansen has found a pair of small tubercles representing them in the adult; and the Collembolan *Anurida*, in which Wheeler and others have seen them for a short embryonic period.

The supraoesophageal ganglion of Insects is likewise developed from three paired masses (Wheeler, Viallanes), the *procerebrum*, *mesocerebrum* and *metacerebrum*. Of these the two latter arise

* Heymons uses the word *protocerebrum*, sensu stricto, for the neuromere of the preantennary segment. The mass consisting of this neuromere combined with the syncerebrum he calls *procerebrum*, but also "*protocerebrum*, sensu lato." It will be called *procerebrum* in this work.

from the neuromeres of the antennal and premandibular segments respectively, the procerebrum representing the protocerebrum together with the complex syncerebrum of *Scolopendra* (Heymons).

With regard to the postoral segments of the head of Insects the evidence is somewhat conflicting. In the development of the Orthoptera investigated by him, Heymons finds three consecutive segments, each with a well developed neuromere and pair of coelomic sacs, which he identifies as belonging to the mandibles and two pairs of maxillae, and which would thus correspond with the appendages so named in *Scolopendra*. On the other hand several observers (Hansen, Folsom, Carpenter and others) have shown that paired structures are present in the mouth of the lower insects, between mandibles and first maxillae, sometimes uniting with the median ligula or hypopharynx but sometimes distinct from it, and presenting (especially in the Thysanura) all the characters of appendages. Thus in *Machilis maritima* Carpenter shows that each ends in two lobes, comparable with the galea and lacinia of the succeeding segment, and bears externally a palp (unsegmented in *Machilis*, Fig. 372, but 3-segmented in *Japyx*). These appendages are named by Hansen *maxillulae* (superlinguae by Folsom). It seems impossible to resist the evidence that they represent a head somite, and Folsom does indeed find, in a later stage of development of the Collembolan *Anurida*, a neuromere corresponding to them. The only difficulty in the acceptance of this view is that Folsom himself finds in an earlier stage of development of *Anurida* no trace of this segment and figures the mandibular and first maxillary segment in juxtaposition. Moreover it is remarkable that this segment should be apparently unrepresented in the development of the Orthoptera so carefully investigated by Heymons. Nevertheless the balance seems to incline in the direction of the true segmental nature of the maxillulae.

Accepting this view we conclude that the maxillulae, first maxillae and labium of insects correspond respectively with the two pairs of maxillae and the poison claws of *Scolopendra*. The fact that the labial (2nd maxillary) segment of Insects is less completely fused with the segments in front of it than they are with one another, affords some confirmation of this view.

In the Crustacea the evidence for segmentation afforded

by the coelomic sacks in other groups fails us, for the mesoblastic somites though segmentally divided contain no coelomic cavities. Among the Malacostraca the supracoesophageal ganglionic mass is laid down in *Crangon* (according to Kingsley) as three consecutive pairs of ganglia, in addition to the optic ganglia, which lie in front of and external to the first pair. Of these three pairs the anterior is preoral, the others originally postoral. The second and third pairs of ganglia are those of the first and second antennae respectively. The development of the corresponding parts in *Astacus* appears to present no essential difference. From these facts, and from the similarity of the shapes of the mandibles and the positions of the paired eyes in Crustacea and Insects, we are led to regard the segments bearing the two pairs of antennae of Crustacea as homologous with the antennal and premandibular segments of insects, the appendages of the latter attaining in the Crustacea a full development which is denied them in Insecta. The mandibular and two maxillary segments of the Crustacea correspond with the mandibular, maxillular and first maxillary segments of Insects, the first thoracic appendages finding their homologue in the labium.

In the lower Crustacea (e.g. *Daphnia*, Fig. 250), the ganglion of the second antennary (premandibular) segment retains a postoral position throughout life.

Turning now to the Arachnida (including the Merostomata) we find that the chelicerae and the six segments of the cephalothorax posterior to them (the segmental significance of the chilaria has been demonstrated by the researches of Kishinouye and Brauer) are represented in development by coelomic sacks, neuromeres and appendages. In front of the cheliceral neuromere is the large paired ganglionic mass of the head lobes. No distinct mesoblastic somite anterior to the cheliceran is found in *Limulus* or *Scorpio*, but among the true spiders evidence of such sacks has been obtained by Kishinouye and others. Indications of paired appendages in front of the chelicerae have been recognized by some observers in the paired origin of the "labrum" in scorpions and spiders, and in prominences formed in relation with the folding in of the brain of spiders, but in neither case is the evidence conclusive.

In most Arachnids the cheliceral neuromere fuses with the

paired mass in front of it to form the supraoesophageal ganglion, the pedipalpi being innervated from the suboesophageal mass.*

The absence of resemblance between arachnid appendages and those of the other groups of Arthropods renders recognition of the homology of the segments exceedingly dubious. We are reduced to the order of the segments, reckoning as first the pre-cheliceral in Arachnida and the preantennal in Tracheata and Crustacea; though when it is remembered how slender the evidence is of the existence of these segments, the insecurity of the proceeding is apparent.

It remains to consider the segmentation of *Peripatus* which is perhaps better marked than that of any other Arthropod. As shown by Sedgwick the coelomic sacks are formed in pairs, and the members of the anterior pair, though postoral at their origin move forward and come to lie in apposition in front of the mouth, forming the first segment. The antennae of the adult are the appendages of the first, the mandibles of the second, the oral papillae of the third segment, and in relation with each of these appendages, as with their successors, a pair of nephridia, opening into the corresponding coelomic sacks is formed.

At no stage of development is the central nervous system of *Peripatus* divided up into distinct ganglia, the lateral thickenings of the ectoderm on either side of the ventral median line "are from their origin continuous from somite to somite," and they are continuous with one another in front of the mouth. The brain of the adult consists of two simple swellings produced behind into posterior lobes. They are in apposition with one another, and there are slight swellings of the lateral cords opposite each of the postoral appendages. The antennary and optic nerves spring from the anterior part of the brain, the nerves to the jaws from the ventral cords as they leave the brain, those to the oral papillae from the ventral cords posterior to the oesophagus.

The relation between the segments of the head (in the case of the Arachnida of the cephalothorax) in the main groups of the Arthropoda, which the evidence at our disposal appears to indicate as probable, are set forth in the following table, though

* It is stated however that in the Phalangidae and the Acarina (Gamasidae) the innervation of the chelicerae is suboesophageal.

		Myriapoda (<i>Scolopendra</i>)	Insecta	Crustacea		Arachnida (<i>Scorpio</i>)	<i>Peripatus</i>
				Trilobita (<i>Triarthrus</i>)	Recent		
Acron	Acron						
1st Metanere	Preantennal Segment		Protocephalon		Protocephalon	Protocephalon	Antennal segment
2nd "	Antennal Segment		Antennal Segment	Antennal Segment	Segment of 1st Antennae	Chelicerar Segment	Jaw Segment
3rd "	Premandibular Segment		Premandibular Segment	Segment of 1st Jaw-Foot	Segment of 2nd Antennae	Segment of Pedipalpi	Segment of oral palpillae
4th "	Mandibular Segment		Mandibular Segment	Segment of 2nd Jaw-Foot	Segment of Mandibles	Segment of 1st leg	
5th "	1st Maxillar Segment		Maxillular Segment	Segment of 3rd Jaw-Foot	Segment of 1st Maxillae	Segment of 2nd leg	
6th "	2nd Maxillar Segment		1st Maxillar Segment	Segment of 4th Jaw-Foot	Segment of 2nd Maxillae	Segment of 3rd leg	
7th "			2nd Maxillar Segment (Labium)			Segment of 4th leg	
8th "						Segment corresponding to chilaria of <i>Limulus</i> . The 'pregenital segment' of Lankester	

the numbers in the first column must, in our view, be regarded as provisional.

It will be seen that in *Peripatus* we have evidence of three head segments, in the Crustacea and Myriapoda (though the case of the Diplopoda is doubtful) of six. In the Insecta a seventh segment, that of the labium, appears to have been added, while in Arachnida the anterior part of the body, here called the cephalothorax, is apparently composed of eight segments.

The term *acron* occurring in the first and second columns of the table was introduced by Janet for the region of the embryo surrounding the mouth (as the *telson* surrounds the anus). It is used here, following Heymons, in a more restricted sense for the region in front of the mouth, containing as its median element the clypeal shield, from which the labrum projects backwards over the mouth. From the epiblast of the acron the syncerebrum of *Scolopendra* is developed. *Protocephalon* is the name given by Heymons to the region occupied by the procerebrum. The acron is regarded by Heymons as the homologue of the prestomial lobe of Annelids. This conclusion leaves out of consideration the case of *Peripatus*, which from the distinctness of the coelomic sacs and the persistence of nephridia cannot be disregarded in discussing the primitive segmentation of Arthropods. It is difficult to believe, notwithstanding the fact that the antennary somites of *Peripatus* are postoral in origin, that mesoblastic structures have ever existed in front of them, and if this is so these somites represent the most anterior segment of the primitive Arthropods, whether differentiated into prestomial lobe and peristomium or not so differentiated. However, as stated in an earlier part of the present work (Vol. I, p. 448), the relation of the prestomium to the segments of the body is far from clear in the Annelids themselves, and we may here confine ourselves to pointing out that the evidence remains conflicting when considered from the point of view of Arthropods.

We have to conclude then that the homology of the segments in Myriapods, Insects and Crustacea, though not free from difficulty is fairly clear; that the homology is obscure in the case of Arachnids, and still more so in that of *Peripatus*. The problem of the relationship between the anterior segments

in Annelids and any group of Arthropods remains, for the present, undetermined.

On another debated point the embryological evidence obtained in recent years also throws light. The anterior antennae of the lower Crustacea, and the antennae of *Peripatus*, Myriapoda and Insecta differ markedly from the appendages of other segments in their simple, many-jointed and generally uniramous character, and these characters in the adults are emphasized by the constantly uniramous condition of the first antennae in the Nauplius larva of Crustacea. The question has arisen—Have we not in these appendages the homologues of the paired tentacles of the prestomium of Annelids?

In the case of *Peripatus* it is possible that we have, but in the other groups the answer of embryology is in the negative. In

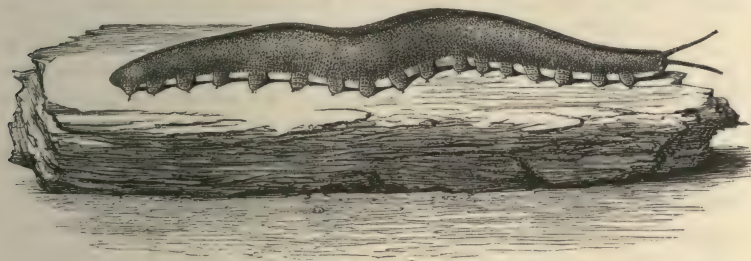


FIG. 230.—*Peripatus capensis* (after Sedgwick).

each they are innervated from the mesocerebrum, and there is evidence in Myriapoda that there has existed at least one segment anterior to that which bears them. Notwithstanding the peculiar character of the first antennae we have to conclude that they, like the other appendages of the head, were originally postoral limbs.

The facts that in *Peripatus* the antennae are the appendages of the first somite, and therefore, presumably, the representatives of the transitory preantennae of the Myriapoda, and that the mandibles belong to the second segment, would seem to place this remarkable genus in a category apart from the other groups of the *Arthropoda*.

As the mouth moves backwards the segments originally postoral become preoral, and their ganglia, fusing together, form the brain or supraoesophageal ganglionic mass of the adult.

The **brain** is thus in all cases a composite structure containing the neuromeres of the preoral segments fused together. The mode of its development in *Scolopendra* would indicate that there is anteriorly, in addition, a median unpaired element (the archicerebrum of Heymons) together with lateral elements (forming, with the archicerebrum, the syncerebrum of Heymons) with which the neuromeres have united, though how this condition is related to that presented by *Peripatus* remains for the present obscure.

The number of neuromeres entering into the brain appears to be two in *Peripatus*, most Arachnids, and in *Daphnia* (Fig. 250) and *Limnadia* (Fig. 241 D) among the Crustacea, three in the Malacostraca, Myriapoda and Insecta.

For the further discussion of the segmentation of the arthropod head and other cognate questions the reader is referred to the literature on this subject quoted at the beginning of the chapter.

The conclusions here arrived at are to a large extent in accordance with those of Heymons, Goodrich and Lankester, but the designation of the segments by a numerical nomenclature, adopted by Lankester, has been as far as possible avoided, because of the uncertainty of deciding in the several groups, which is the first segment.

The Eyes of Arthropods. The eyes of *Peripatus* are vesicular structures which arise by invagination of a portion of the brain rudiment (while it is still part of the skin) with which they retain their connexion by the optic nerve. In this they appear to resemble the simple eyes of Arachnida.

Little has been ascertained throwing light on the origin of the unpaired "nauplius eyes" of the lower Crustacea.

Apart from *Peripatus* the simplest form in which the paired eyes are met with in Arthropods is that presented by the *stemma* or *ocellus* of Insects (Fig. 231). The chitinous cuticle is thickened to form a lens, and beneath this the cells of the hypodermis are disposed in a cup-shaped manner, the adjacent cells being highly pigmented. The cells in the floor of the cup form the retina, and are in connexion with the nerve; while the transparent ends of the surrounding cells, bending over the retina from the sides, form a clear medium, which has been called the vitreous body, intervening between the retina and the lens. It appears evident from the arrangement of the parts of such a simple eye that the light entering through the lens is focussed on the layer of retinal cells, and hence that some representation

of the outer world may be conveyed to the brain. From the small number of the cells in the recipient layer, however, it would appear that the perception of surrounding objects thus conveyed must be of a low order.

The eyes of Myriapods and the Thysanura consist of a number of such ocelli, collected into groups.

Although we have to conclude that the Insecta and Crustacea belong to two distinct divisions of the phylum; the highly developed **compound eyes** of each agree closely in the plan on which they are formed. They may be derived from a group of ocelli, the number of which is greatly increased, while the number of cells in each is decreased (Grenacher). Each ocellus, or single eye, which thus with its fellows makes up the compound eye, is known as an *ommatidium* (Fig. 232). They are usually disposed so as to present to the exterior an even convex surface.

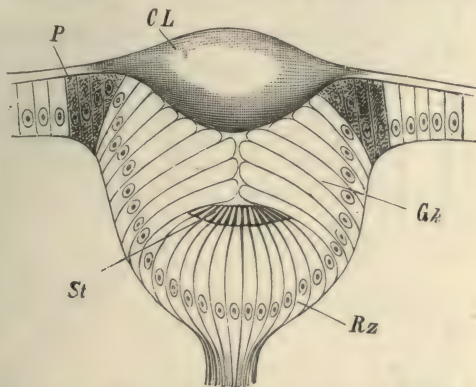


FIG. 231.—Section through the ocellus of a *Dytiscus* larva (after Grenacher, from Claus). *CL* corneal lens; *Gk* the subadjacent hypodermis cells forming the "vitreous body"; *P* pigment in the peripheral cells of the latter; *Rz* retinal cells; *St* cuticular rods of the latter.

ocelli, the number of which is greatly increased, while the number of cells in each is decreased (Grenacher). Each ocellus, or single eye, which thus with its fellows makes up the compound eye, is known as an *ommatidium* (Fig. 232). They are usually disposed so as to present to the exterior an even convex surface.

The minute structure of the eyes of *Branchipus* and *Palaemon* may be taken as typical of the compound eyes of Arthropods (Fig. 232). Each *ommatidium* is limited externally by a corresponding portion of the transparent cuticle which may be thickened in the centre to form a biconvex lens (*cl* in A), as in the faceted eyes of Insects, Decapods, Isopods, etc., or maintain a uniform thickness, as in *Branchipus* (*c* in E). Under it lie the two *corneagen* or *lentigen* cells by which it is secreted. Beneath are four (2 in the Isopod *Sphaeroma*) cells, the *vitellae* or crystal cells (*kz*) grouped about the *crystalline cone*, the product of their secretion. In *Branchipus* its shape is fusiform, but it is often conical, with the point directed inwards. In *Palaemon* (Fig. 232, A *k* and *k*,) it is represented by two distinct refractive

bodies, an outer and inner. About the vitrellae 2 (or 4) pigmented cells (cf. Fig. 233) are disposed. They are the *iris pigment cells* (the distal retinular cells of Parker). The vitrellae abut internally against a group of elongated cells

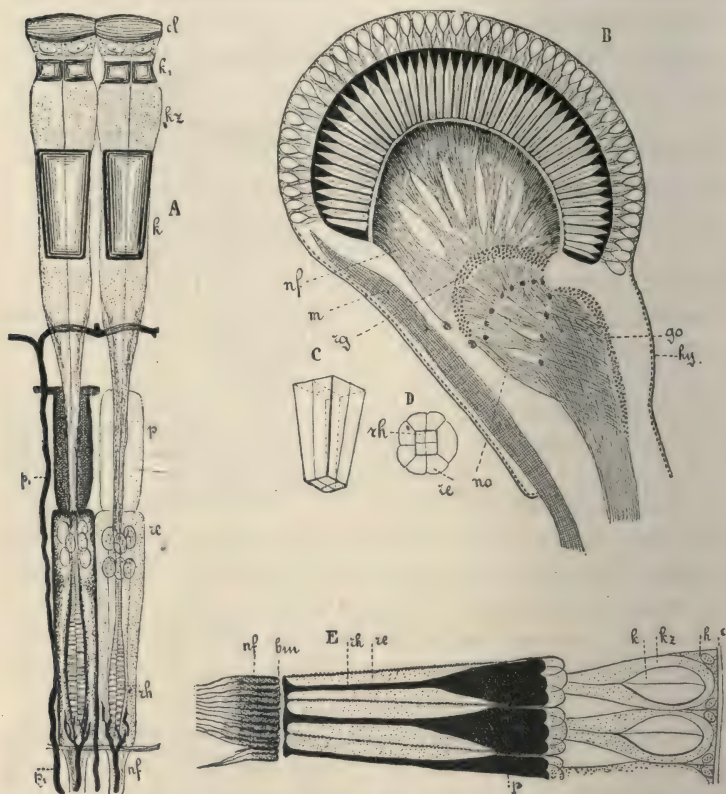


FIG. 232.—The compound crustacean eye. A two ommatidia of *Palaemon squilla*. The pigment is removed from the right-hand ommatidium, consisting of four elements. C Isolated crystalline body of an ommatidium, consisting of four elements. D Transverse section through a retinula about the middle of its length. B Section through the stalked eye of *Branchipus*; E two ommatidia of the same on a larger scale.

bm basal membrane; c cornea; cl corneal lens; go optic ganglion; h (in E) lentigen cells; hy unmodified hypodermis; k crystalline cone; k outer crystalline body; kz vitrellae; m muscle; nf nerve fibres; no optic nerve; p (in E) pigment in retinula cells, (in A) pigmented hypodermis cells; p, (in A) mesoblastic pigment strands between the ommatidia; re retinular cells, deprived of pigment in D; rg retinal ganglion; rh rhabdom.

(From Lang's Textbook, A C and D after Grenacher; B and E after Claus.)

forming the *retinula* (re) which constitutes the innermost element of the ommatidium. The retinular cells in varying number (4 in *Mysis*, 5 in *Branchipus*, 7 in *Palaemon*) are arranged about the optical axis of the ommatidium, and, like the vitrellar and

lentigen cells of the external layers, are in relation with a refracting element, the *rhabdomere*, which forms their axial border. They are also abundantly invested by black *pigment*. The several rhabdomeres of a retinula make up the *rhabdom* (Fig. 232, A and D *rh*). Internally the retinular cells are continuous through apertures in a *basement membrane* (*bm*) with the nerve fibres of the optic ganglion. The crystalline cone (C) like the rhabdom bears evidence of being divided longitudinally. In some cases (*Sphaeroma*) the rhabdom contains a central space, occupied by one or two *hyaline cells* (Watase). Moreover the rhabdomere has been found in some cases (Schizopoda, Decapoda) to present very fine striations perpendicular to its margin (Fig. 232 A *rh*) which are regarded by some authors as the ultimate ends of nerve fibrillae. The distribution of the pigment in both sets of cells is, as we shall see, dependent in some animals on the degree of illumination to which the eye is subjected.

Beside the cells forming the ommatidia proper other hypodermic cells in varying number are present in the interspaces between them (Figs. 232 A *p*, and 233, 6). These (*accessory pigment cells*) may contain flakes of pigment which is not black but white by reflected and yellow by transmitted light. The function of this pigment appears to be not to absorb, but to reflect the light. It forms the *tapetum* of crustacean eyes. In the eyes of Insecta, adapted for vision by night (see below), tufts of minute tracheae invest the retinulae, and by their shining surfaces likewise serve as a tapetum (Exner).

According to Lord Avebury some 4,000 ommatidia compose the eye of the common house-fly, while that of a Dragon-fly (*Aeschna*) contains 20,000.

The mode of working of the compound eye was explained in part by the theory of mosaic vision first propounded by Johannes Müller. The only direction from which the light is able to penetrate to the retinula of an ommatidium, ensheathed in pigment in the manner above described, is that in and near the line of its axis. The light which thus enters, concentrated on the pigmented retinular cells by the refracting media of the ommatidium and reflected from the surrounding tapetum, will set up changes in them, according to its nature, and give rise to a corresponding stimulus in the nerve fibres with which they are

connected. Thus the retinula of one ommatidium receives a single resultant impression from the light which reaches it. But the adjacent ommatidia being directed to a different, though

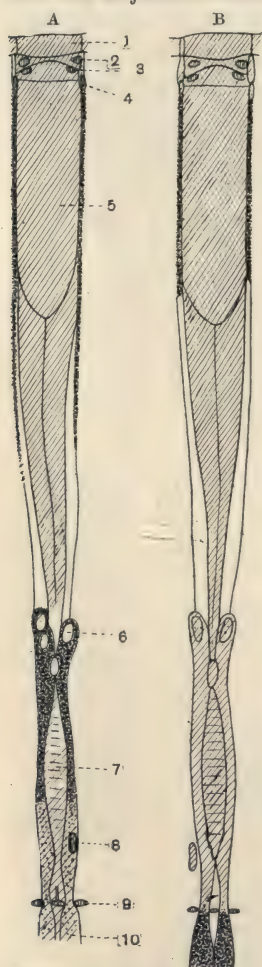


FIG. 233.—Longitudinal sections of two ommatidia of *Astacus fluviatilis* showing the arrangement of the pigment as influenced by light (A) and by darkness (B) (after Parker); 1 cornea; 2 nucleus of corneagen cell; 3 nucleus of vitrella; 4 nucleus of iris pigment cell; 5 crystalline cone; 6 nucleus of cell of tapetum; 7 rhabdom; 8 nucleus of retinal cell; 9 basement membrane; 10 retinal nerve fibre.

adjoining, region of the outer world, may transmit a different impression, and the stimuli from all the ommatidia which make up a compound eye will correspond in greater or less degree to the whole of the visible outer world which subtends their several optic axes. The sum of the resulting images which we may thus suppose to be transmitted to the brain may be compared to a mosaic in which the effect is given by a large number of separate pieces, of one size and each of uniform colour. It is evident on the one hand that the smaller the angle of each ommatidium and the larger the number of ommatidia in an eye, the more perfectly will the resulting stimulus correspond with the details of surrounding objects. On the other hand the loss of light by absorption in the pigment of such an eye is very great and increases for each unit of surface with the number of ommatidia it contains.

Our knowledge of the functions of the compound eyes of Arthropods has been extended by the work of Exner, Szczawinska, Chun, Parker and others. It has been shown that in a variety of Arthropods inhabiting shallow water, or the land, the pigment contained in the iris pigment cells and the retinulae occupies very different positions in accordance with the degree of illumination (Fig. 233). In bright light the pigment invests the ommatidia in the manner described above, and though a

great deal of light is absorbed by the pigment some reaches the retinulae, and forms the erect mosaic or "*apposition image*" in the manner indicated. But when the eyes of these animals are fixed by reagents after being exposed to darkness, it is found that the pigment blinds which separate the ommatidia from one another are withdrawn. The pigment in the iris pigment cells is drawn up towards the cornea, that in the retinulae has retreated below the basement membrane towards the nerve fibres.* It has been shown that under these conditions the ommatidia no longer act separately, but that a combined image is thrown on the reticular layer, the crystalline cones being so disposed that the light from a given point falling on a considerable area of the eye, no longer obstructed in its course by the blinds of pigment, is brought to a focus on that layer. In this manner an erect "*superposition image*" is formed, the rays refracted by a large number of crystalline cones being superposed at the focus on the retina, and a stimulus far stronger in proportion to the intensity of the illumination than that of the apposition image, though probably much less distinct in details, is given to the retinulae. The eyes of insects such as fireflies and many moths are permanently in this condition, and are "day blind." On the other hand the eyes of butterflies have the pigment permanently expanded, and are "night blind."

A very interesting confirmation of these results has been furnished by the beautiful researches of Chun on the pelagic Schizopods inhabiting the dark waters of the ocean at a depth of 300–600 fathoms (Fig. 290). In these the reticular pigment has disappeared altogether, while the distribution of that of the iris pigment cells varies in different parts of the eye, according as the ommatidia are directed sideways (lateral eye) towards objects which may be illuminated by the phosphorescent organs carried by the animal itself, or forwards (frontal eye) into the dark region from which the rays of these organs are by their position excluded. In the frontal eye moreover the number of retinulae is far in excess of that of the crystalline cones, a condition which is in harmony with the theory of the formation of a superposition image, but unmet by the mosaic theory.

* As in the pigment cells of the frog, the chromatophores of Decapods, etc., the movement of the pigment takes place *within* the cell, and the shape of the latter is unaffected by the movement.

The lateral eyes of *Limulus* offer an interesting intermediate condition between the compound eye and a group of simple eyes. They are raised reniform areas on the sides of the cephalothorax, the cuticle over them being transparent. They consist of a number of pits in the hypodermis (Fig. 234) the bottoms of which are occupied by bulb-like retinulae consisting of some 10–15 cells grouped about a central ganglion cell. The inner margin of each retinular cell is highly refracting. The group of these refracting bands in a retinula evidently corresponds

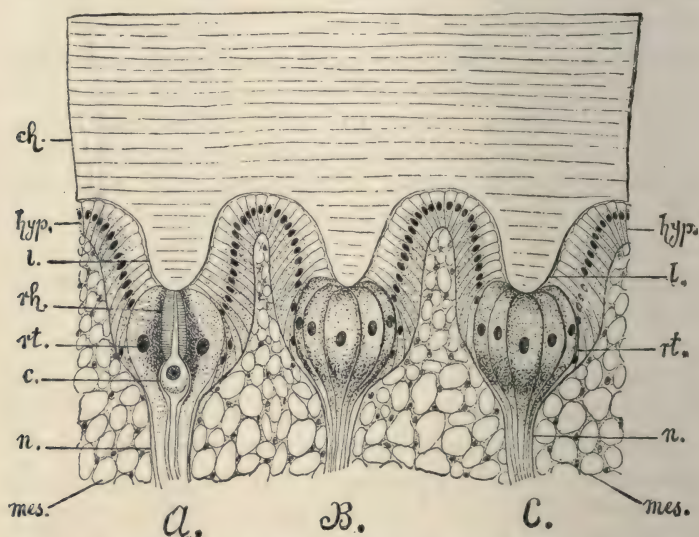


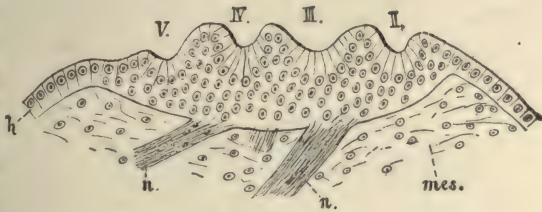
FIG. 234.—Three ommatidia of the lateral eye of *Limulus* (after Watake). In A a retinula is divided longitudinally; in B and C whole retinulae are represented. c central ganglion cell; ch cornea; hyp hypodermis; l lens; mes mesoderm; n nerve; rh segment of the rhabdom; rt retinula.

with the rhabdom of an ommatidium of the compound eye. The cells are continued below the basement membrane, as is the central ganglion cell, into nerve fibres. The columnar cells of the hypodermis surrounding the retinulae and forming the walls of the pit are bordered with pigment. The cavity of the pit is filled by a rounded process of the under surface of the cuticle, which apparently acts as a lens, but each is continuous above with the common investment of cuticle forming the cornea.

The lateral eyes of Scorpions (Fig. 235) form a group on either

side of the cephalothorax consisting of 2-7 distinct eyes, the number varying according to the species. The whole group however passes through a stage in development which strikingly resembles the permanent condition in *Limulus* (Fig. 234). The hypodermis is thickened and pigmented over a considerable area, and the surface becomes invaginated to form pits corresponding in number to the separate eyes of the adult. The cells

a.



B.

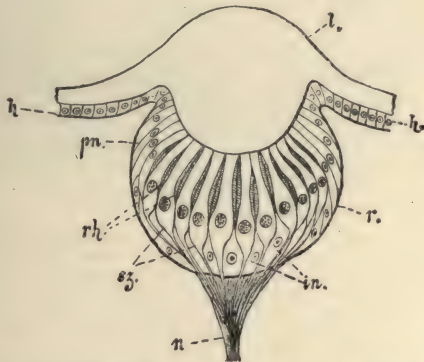


FIG. 235.—Sections through the lateral eyes of *Scorpio* in two stages in the development. *A* earlier, *B* a single element at a later stage; somewhat diagrammatic (from Korschelt and Heider, after Parker and Laurie); I-II-V optic invaginations; *h* hypodermis; *in* interneural cells; *l* lens; *mes* mesodermal tissue; *n* optic nerve; *pn* perineural cells; *r* retina; *rh*, rhabdom; *sz* retinal cells.

between the pits assumes the ordinary character.

According to Kishinouye the posterior median (Fig. 237, *B*) and the lateral eyes of Spiders likewise arise as simple ectodermal depressions, in which case they would belong to the same category as the lateral eyes of *Limulus* and *Scorpions*.

The paired arthropod eyes hitherto considered belong to a

type to which the name *monostichous* * has been applied (Lankester). They are all to be regarded as developments of a single layer of the hypodermis.

The median eyes of *Limulus* and *Scorpio* (Fig. 237), and the anterior median or "principal" eyes of Spiders (Fig. 237, *A*) belong to a different type, the *diplostichous*. In these eyes two layers of hypodermis are concerned in the formation of the optical apparatus (Fig. 236). They are formed in ontogeny by the folding in of the hypodermis from the side of the area which will be occupied by the eye. The outer of the two layers thus involuted becomes

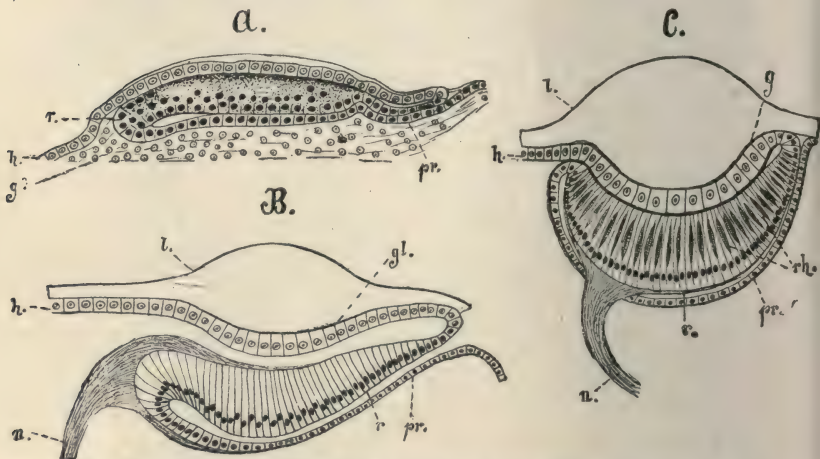


FIG. 236.—Section through the median eye of *Scorpio* in three stages of development. From Korschelt and Heider. *A* after Parker, *B* and *C* diagrammatic. *g* ? brain (?); *gl* (*g* in *C*) vitreous body; *h* hypodermis; *l* lens; *n* optic nerve; *pr* postretinal layer; *r* retina; *rh* rhabdom.

the retina (*r*, Fig. 236), its columnar cells secreting rhabdoms (*rh*), and the inner, when it persists, the post-retinal membrane. The layer of hypodermis external to the fold becomes the vitreous body and secretes the lens. The nerve, by secondary shifting of its position, enters the under surface of the retina. There are thus three layers of hypodermis concerned in the development of the diplostichous eye, though the dioptric layers are formed from only two of them. The involutions from which these eyes are formed are closely associated with those forming the brain, but the morphological significance of this mode of development is quite obscure.

* *στίχος*, a row, line.

The optical arrangement of the lateral and median eyes of Scorpions and Spiders and of the median eyes of *Limulus* is such as to throw a reversed image on the retina.

The development of the lateral eyes of the Scorpion supports the view of Lankester and Bourne that they are derived from an eye very like that of *Limulus*, the several elements of which have become separate. It is easy to imagine, on purely theoretical grounds, that the compound eyes of Insects and the Crustacea might be derived from an eye such as the lateral eye of *Limulus* by the opposite process, namely by the specialization of the several depressions into ommatidia, their increase

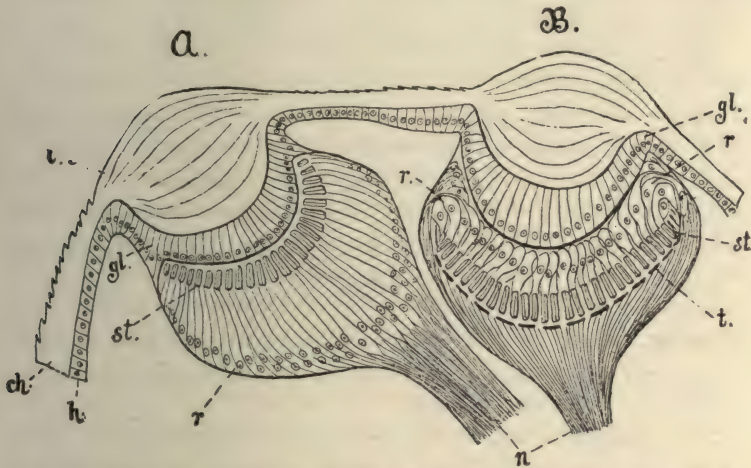


FIG. 237.—A anterior, B posterior median eyes of a spider (diagrammatic from Korschelt and Heider, after Grenacher and Bertkau). *ch* chitinous cuticle, passing into cuticular lens (*l*); *gl* vitreous body; *h* hypodermis; *l* lens; *n* optic nerve; *r* retina; *st* rod; *t* tapetum.

in number, and closer aggregation. However the facts at our disposal seem rather to point, as above indicated, to the origin of compound eyes of Insects in a different manner, i.e. from groups of distinct ocelli such as are found in Myriapods. The morphological nature of the paired eyes of Crustacea is discussed on p. 249.

Statocysts. The open or closed saccular organs of the Crustacea, containing sensory hairs, have generally been named otocysts. It is now recognized that they perform the function of statocysts (cf. p. 350), though they may possibly possess

an auditory function as well. They are described on p. 350. Another possible function of these organs, suggested by Balfour, is the perception of the vibrations set up in the water by other animals swimming in their vicinity.

Of a wholly different structure are the *chordotonal organs* of Insects to which an auditory function has been assigned. They are groups of elements, widely scattered over the body, each of which consists of a delicate rod contained in a tubular pit sunk beneath, and opening at the surface. The rod is continued into a ganglion cell at the base of the pit, and a mechanism exists for maintaining the walls of the tube in a tense condition. The *tympana* on the legs of insects are modified areas of cuticle in relation with groups of such organs (p. 636).

Tactile setae in relation with ganglion cells are widely found on the extremities, especially the antennae of Crustacea and Insects; and many organs occur, especially in Insects, evidently of a sensory nature, but on the special function of which we can only vaguely surmise. Some are doubtless olfactory.

Complementary to the organs of special sense are other organs widely found among Arthropods such as the **light-producing organs** of many Insects (fire-flies, etc.) and Crustacea (Copepoda, some Ostracoda, Euphausiidae, some Decapods, etc.), the **stridulating organs** of spiders, grasshoppers, cicadas and decapod Crustacea, and organs for diffusing special odours which are widely found among Insects.

The **respiration** of Arthropods is generally effected by branchiae or by tracheae. The Copepoda, most Ostracoda and some Cladocera have no specialized respiratory organs, and in *Birgus latro* and, in less degree, in some other terrestrial Decapods the branchial chamber is, as pointed out by Semper, modified into a sort of lung (p. 540). The branchiae are originally (with the exception of the tracheal gills of some larval Insects and the gills of sessile Cirripedes, and some Ostracods) appendages of the limbs. The lung-books of the Arachnida, although modified for breathing air, are, as the interesting researches of Simmons on Spiders, and Brauer on *Scorpio* have shown, to be regarded as modifications of such branchiae as are borne on the abdominal appendages of *Limulus*.

Tracheae are tubular involutions of the outer layer of the body by means of which air is carried to the tissues. In members

of all the great divisions of the Arthropoda which live in air tracheal structures have been developed. Those of *Peripatus*, the Myriapods and Insects need not be further mentioned here. In the Arachnida tracheae are present in addition to the lung-books, or as the sole respiratory organs. Even the Crustacea furnish us with an incipient tracheal system in the tufts of branching air-tubes found in the abdominal legs of some Isopods (wood-lice) (Fig. 297).*

The **sexes** are separate in the great majority of Arthropods, but the Cirripedes, having adopted a sessile habit in the adult stage, are hermaphrodite, and some genera of them present the remarkable phenomenon, discovered by Darwin, of the existence of a minute and short-lived "complementary male" in addition to the hermaphrodite individuals of their species. Certain of the Isopoda, parasites on fish or other Crustacea, are protandrous hermaphrodites (cf. pp. 484 and 490).

Parthenogenesis occurs as a constant feature of the life-history in many genera of the Phyllopoda and Ostracoda among the Crustacea, and of the Hymenoptera and Hemiptera among Insects. The number of generations arising in this manner before the recurrence of a sexual phase may be large, as in *Aphis*, and many genera of the Entomostraca; in some of the latter indeed (*Cypris reptans*, *Limnadia Hermannii*), as well as in some Insects (cf. p. 640), males are unknown.

Among the Crustacea the parthenogenetic females are usually similar in their general structure to those which are capable of being fertilized, but in Insects the members of the life-cycle are frequently dimorphic, or (*Phylloxera*) trimorphic, and differ so considerably from one another that, before their life histories were ascertained, they were referred to distinct genera.

The **eggs** of Arthropods are usually heavily laden with yolk. In some few Crustacea, in which there is little yolk stored in the egg, the cleavage is complete, and in the pelagic Decapod *Leucifer* the hypoblast is formed by a normal process of invagination. But in the great majority of Arthropods the course of the segmentation is modified owing to the presence of the yolk. It is generally stored in the central region of the egg and though segmentation may be complete at first the large yolk-laden central spheres often fuse together subsequently; or the

* Compare the development of tracheae in the *Velellidae*, vol. I, p. 142.

segmentation may go on superficially from the beginning, leaving the yolk mass undivided.

In some cases (*Mysis*, *Scorpio*) the blastodermic layer is confined after its formation to one pole of the egg—the *telolecithal* eggs of Balfour; but in Insects and many Crustacea it entirely surrounds the yolk—an arrangement which hardly occurs outside the Arthropoda. For such eggs Balfour adopted the name *centrolecithal*.

The remarkable phenomenon known as *polyembryony*, presented by some parasitic Hymenoptera, in which the egg divides up and gives rise directly to a brood (12–1,000) of new individuals, is referred to on p. 641.

Associated with the abundance of the yolk in the interior of the egg is the early disappearance of the mesoblastic somites, and the consequent difficulty in tracing the development of the organs derived from the coelom.

In *Peripatus*, the Myriapods and apterygote Insects the endoderm furnishes the greater part of the alimentary canal, as in most other animals; but in some of the higher Arthropods the endodermal portion, the mid-gut proper, is much reduced in length, the stomodaeal and proctodaeal portions (fore- and hind-guts) being proportionally elongated. Thus in some Decapods and Isopods only the hepatic diverticula and a small part of the adjoining central tract of the alimentary canal are endodermal. In Insects the tract extending from the crop to the beginning of the ileum (including the hepatic diverticula but not the malpighian tubes) is usually named mid-gut, the chitin-lined regions in front and behind being formed by the ectodermal involutions. The embryological evidence on this point is however conflicting, and Heymons is even inclined to the view (though this meets with opposition in competent quarters) that the endoderm, though taking part in the formation of the alimentary canal of some of the lower Insects (*Lepisma*) is entirely unrepresented in the adults of the higher groups, and that the whole alimentary canal is formed in them by the meeting of stomodaeum and proctodaeum.

In connexion with the development may be mentioned the remarkable property of the arthropod body, which it possesses, in common with other groups of the Metazoa, of *reproducing parts lost* by injury or amputation. Only the limbs and eye-stalks are thus reproduced, and in the case of the thoracic appendages of the Crustacea only the parts distal to the

basipodite. At the ecdysis following the injury it is found that the lost part has been formed again, in miniature, in the stump of the appendage, and in succeeding moults it grows more rapidly than other parts of the body. In some cases the new limb is precisely a repetition of the lost one, but it is often found that the segmentation is different. Thus a normally 5-jointed tarsus of a cockroach is often replaced by a 4-jointed one.*

The divisions of the Arthropoda adopted in the present work are as follows :—

Class I. **Crustacea.**

Class II. **Onychophora.**

Class III. **Myriapoda.**

Class IV. **Insecta.**

Class V. **Arachnida.**

* For further details, and reference to the literature of this subject see H. H. Brindley, On certain characters of reproduced appendages in Arthropoda, particularly in the Blattidae, *P.Z.S.*, Dec. 13, 1898.

CHAPTER V.

CLASS I. CRUSTACEA.*

Aquatic Arthropoda usually breathing by means of gills, with two pairs of antennae and numerous pairs of frequently bi-ramous legs on the thorax and on the abdomen.

The crustacean body is usually more or less distinctly divisible into three main regions—the head, which contains a constant number of segments, and the thorax and abdomen in which the number varies considerably in the several groups.

In recent Crustacea the **head** usually differs from the succeeding parts of the body in the absence of external separation between the segments, although in the fossil Trilobites the more or less complete grooves which traverse it appear to bear witness to its original segmentation (Fig. 243). It differs also in the character of its limbs, and in the absence from them of branchial lobes.

The **thorax** usually bears the main locomotory appendages. Its segments are usually larger than those of the rest of the body and though often distinct they are generally less movable on one another than those which follow. The **abdomen** usually consists of narrower and more mobile segments and in most groups carries appendages, which differ in character from those of the thorax. In many Entomostraca however (*Apus*, Copepoda, etc.) the distinction between thorax and abdomen is little marked. The orifices of the generative organs are frequently situated near the junction of thorax and abdomen.

The groove separating the head from the thorax is well marked in the Trilobites, the Phyllopods, *Nebalia*, as well as in the larval forms of some Copepods, and of several of the Malacostraca,

* In addition to the literature cited below the student is referred, for further details, to the work of A. Gerstaecker, completed by A. E. Ortmann, on Crustacea in *Bronn's Thierreich*, Leipzig, 1866–1901, and to the section on Crustacea by K. Heider, in Korschelt and Heider's *Text-book of Embryology*.

but in many cases fusion has occurred between the head and one or more of the anterior thoracic segments to form a **cephalothorax**. This fusion may depend simply on the obliteration of the grooves between the segments, as in Copepoda and the Isopods and Amphipods, but it is frequently associated with the development of a structure characteristic of many groups of Crustacea, the **dorsal shield**. This is primarily a reduplication of the integument of the head, extending backwards over the body, and more or less completely enveloping it. In the Cladocera (Fig. 252) it forms an incomplete bivalve shell enveloping the hinder part of the body, but the head is not enclosed by it. In the Ostracods (Fig. 253) and some Branchiopods the whole of the body can be enclosed between the valves of the shell, and shut up within it by the action of an **adductor muscle** (Fig. 253, 13) passing between them.

Although the dorsal shield is primarily a fold of the integument of the head, the base of the fold may extend backwards (as in Decapods) involving some or all of the terga of the thoracic segments, and in this manner emphasizing the fusion of the two regions in the cephalothorax.

The terms **carapace** and **shell** have been used in different senses. They may imply the fused terga of the head and of a variable number of thoracic segments; but are sometimes synonymous with "dorsal shield."

The fold contains blood sinuses, and may, when the shell is thin, form an important respiratory organ. In the Entomostraca the coils of the excretory organ, hence known as the **shell gland**, are included in it (Fig. 252, *Sd*). In the Cirripedes, as will be explained more fully under this group, a large part of the tissues of the head become, in the adult, included in the fold.

An *upper lip* (*hypostoma*) and *lower lip* are generally present, in front of and behind the mouth. The latter may be conspicuously bilobed, but it is always distinct from the appendages in the Crustacea.

Appendages. With the exception of the first antennae the appendages throughout the body, and in the several groups, though modified to subserve the most varied functions, conform in a remarkable manner to a common type—the *biramous limb* of the Crustacea. This consists of a shaft or stem—the *protopodite*, usually regarded as composed of two segments, the proximal or *coxopodite*, articulating with the segment of the

body, and the distal or *basipodite*. To the outer end of the latter are articulated two usually segmented branches, an inner and outer, the *endopodite* and *exopodite* respectively. The segments both of the protopodite and the endopodite may be produced towards the median plane of the body into lobes or *endites* (Fig. 238 *a*, *en*). Similarly the segments of the protopodite may be produced on their outer borders into *exites*, or *epipodites*, one to three in number (*ep*).

Hansen has shown that in the biramous limbs of Calanidae and *Argulus* (the case of the Phyllopods cited by him appears less convincing) the protopodite (or *stem*) is composed, not of two, but of three segments; and this he regards, with much probability, as a primitive crustacean condition. When only two segments are present, the proximal segment may have fused with the body (Decapods) or with the second, forming the coxopodite.

There are some, though very few, indications of the occurrence of the biramous limb in other groups of Arthropods; e.g. the abdominal limbs of *Limulus* (vide infra) and the first and second maxillae of Insects.

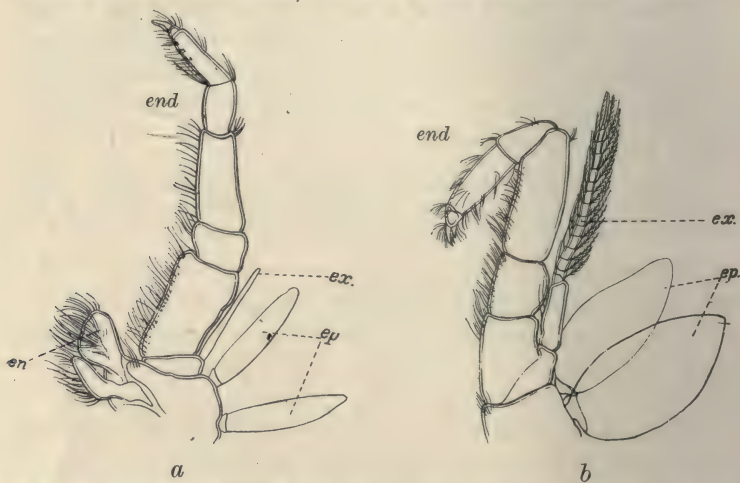


FIG. 238.—The first (*a*) and second (*b*) left thoracic legs of *Anaspides*. *en* endite; *end* endopodite; *ep* epipodites; *ex* exopodite. (After Calman.)

The appendages of the head. The *first antennae* of the Crustacea, the homologues, as we have seen reason to suppose, of the antennae of the Myriapoda and Insects, are usually, like them, simple many-jointed appendages. They are never biramous in the early larval stages, though in some of the Malacostraca they may acquire one (e.g. *Gammarus*, Fig. 239) or even two (Stomatopoda, Fig. 228, and some Decapods) accessory flagella. They are usually abundantly supplied with

tactile and olfactory sense organs, and in many Malacostraca carry an otocyst (cf. p. 350) in the basal segments.

The *second antennae* are generally biramous. Beside their tactile function they are often powerful swimming appendages. In the anostracous Phyllopods numerous secondary lobes are developed in the male and they are prehensile. In the Malacostraca the exopodite has often the form of a simple scale, which however is (in the development of *Euphausia*) derived from an articulate flagellum. In the nauplius larva a masticatory lobe is present and the appendage is paroral, a condition appar-



FIG. 239.—*Gammarus pulex* (after G. O. Sars). *A'*, *A''* the two antennae; *F'*, *F7* the first and seventh ambulatory legs (thoracic legs 2-8); *K* maxilliped; *S7* first abdominal legs.

ently permanent in the Trilobites, in which group they formed the first pair of jaws. The antennal excretory gland opens when present on the coxopodite, or when there are three segments of the protopodite, on the second of them.

The *mandible* is characterized by the development of the coxopodal endite into a cutting and masticatory blade, the remainder of the appendage constituting the mandibular palp. This usually consists of the basipodite and a few-jointed endopodite, but in some Copepods (Fig. 260) and Ostracods (Fig. 253) an exopodite is found in addition. The palp is in some cases absent altogether.

The *two pairs of maxillae* (Fig. 240 *c* and *d*) are generally short and jaw-like, consisting mainly of the protopodite and a short endopodite, the segments of which are produced into cutting blades (endites); a simple lobed exopodite is however frequently present. Hansen concludes that the two inner blades of the first maxilla belong to the 1st and 3rd segments of the protopodite. The *maxillary excretory gland* (the "shell gland" of many Entomostraca) opens on the 2nd maxilla.

Often associated with the formation of a cephalothorax, modification of one or more of the anterior thoracic limbs has

occurred in many groups, resulting in their loss, in varying degrees, of a locomotory function, and their adaptation to subserve the transference of food to the mouth. The thoracic limbs thus modified are known as *maxillipeds*.

The **appendages of the thorax** vary greatly in number and shape. In the Polycopidae (Ostracoda) they are absent altogether, locomotion being effected entirely by the limbs of the head; in other Ostracoda there are two pairs, in the Cladocera 4-6, and in the Phyllopoda 11-19 pairs. In the Malacostraca the number is almost constantly (except in obviously degraded

forms) eight. In the Apodidae there are 40-63 pairs of post-cephalic appendages, presenting a gradual transition in form and size; but the presence of the opening of the genital duct on the segment bearing the 11th permits us to regard the eleven anterior as thoracic.

The modifications which befall the epipodites of the thoracic limbs present an interesting series. They are generally branchial in character and may be simple lobed plates (Phyllopoda, *Anaspidetes* (Fig. 238), Amphipoda) or variously

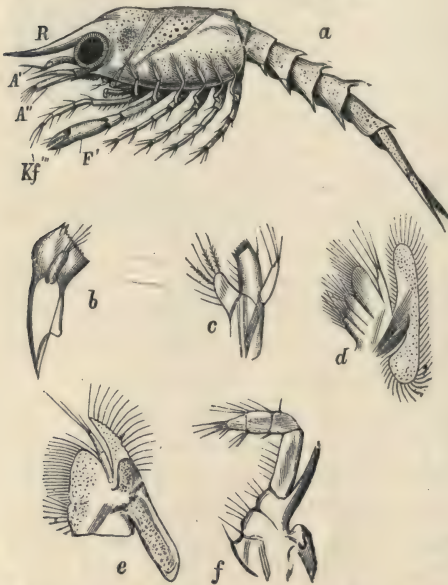


FIG. 240.—Larva of Lobster (after G. O. Sars). *a* the larva seen from the side; *A'*, *A''* first and second antennae; *F'* the chelate first ambulatory legs (4th thoracic). Like the other thoracic limbs they carry exopodites in the larva. *Kf''* third maxilliped; *b* mandible, with palp; *c* anterior or first maxilla; *d* posterior or second maxilla (with scaphognathite); *e* and *f* first and second maxillipeds.

subdivided (Schizopoda, Decapoda); but in certain groups of Malacostraca ("Peracarida," cf. p. 455) the epipodites of certain of the legs appear to have become modified in the female as *oostegites*, to form, together with their fellows, a brood pouch beneath the thorax, in which the young are protected.

Except in some of the Branchiopoda (as *Apus*, to which

allusion has just been made) **abdominal legs** are not found in the Entomostraca, but in the Malacostraca they are nearly always present as biramous swimming limbs (*pleopods*), the posterior pair (*uropods*) often forming with the telson the powerful caudal fin. In Isopods and Stomatopods the respiratory function is carried on by the abdominal appendages.

The central nervous system. In the Phyllopoda (Fig. 241 D) the ganglia of the ventral chain are wide apart and each is connected with its fellow by double transverse commissures. There is a pair to each pair of postoral appendages. Many of the lower Malacostraca present little advance on this arrangement, but various degrees of concentration are presented by the several groups.

The composition of the supraoesophageal ganglionic mass differs, as pointed out above (p. 323), in the Malacostraca and in some members at least of the Entomostraca. In the former there is evidence that three neuromeres join with the optic ganglia to form the brain. The middle and the posterior neuromeres give off nerves to the first and second antennae respectively.

In the Branchiopod genera *Daphnia* and *Limnadia* the neuromere of the second antennary segment retains its post-oesophageal position (Figs. 241 D and 250) and forms the first ganglion of the ventral chain. Hence we have in recent Crustacea two stages of the process by which the compound brain of Arthropods is formed; one (represented by *Daphnia* and *Limnadia*) in which the second antennary neuromere is post-oesophageal, the other, the malacostracan stage, in which it has become pre-oral, and merged in the mass of the brain, although in many Malacostraca the paired ganglia forming it are apparently connected by a transverse commissure (Fig. 241 y) passing behind the oesophagus.

Frontal sense organs. Attention may here be drawn to small paired sense organs, found in many Entomostraca on the front of the head. In the larva of *Apus* they consist of papillae with dilated bases.

The **unpaired or median eye** often called the *nauplius eye* is a characteristic feature of the Crustacea, occurring alone or in association with the compound eyes in all the groups of the Entomostraca, and in the larval stages of the Schizopoda, Decapoda and Stomatopoda among the Malacostraca. In some Copepods it consists of 3 groups of cells, a median ventral and

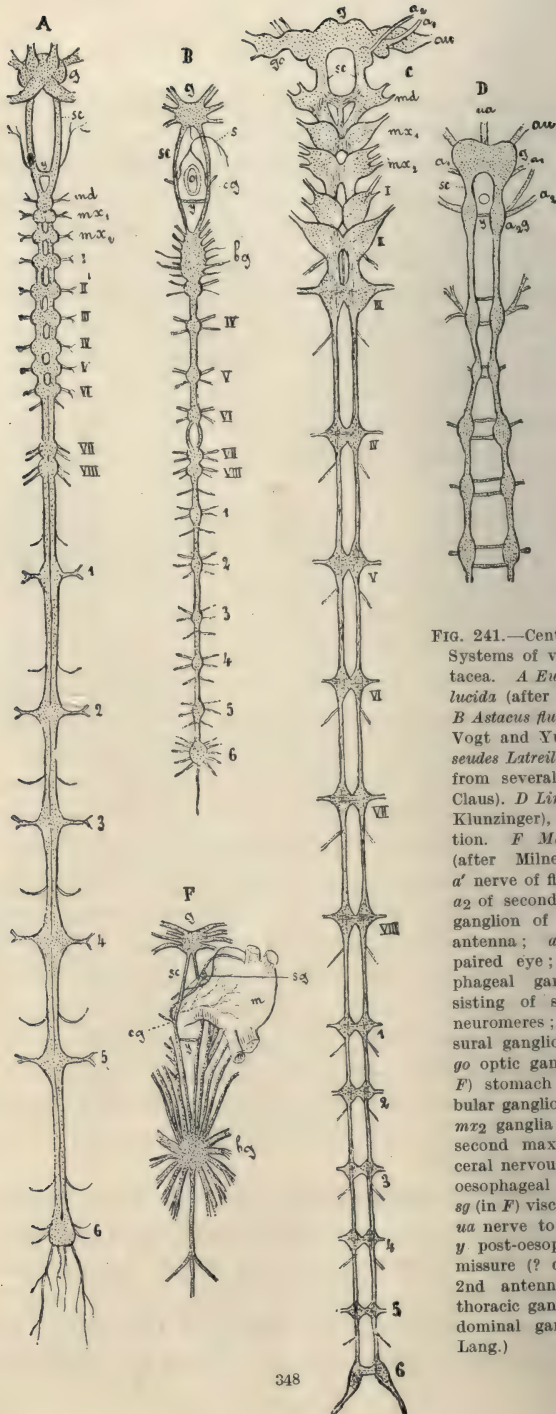


FIG. 241.—Central Nervous Systems of various Crustacea. *A Euphausia pelucida* (after G. O. Sars). *B Astacus fluviatilis* (after Vogt and Yung). *C Apseudes Latreillii* (combined from several figures by Claus). *D Limnadia* (after Klunzinger), anterior portion. *E Maia squinado* (after Milne Edwards). *a'* nerve of first antenna; *a₂* of second; *a_{2g}* (in *D*) ganglion of the second antenna; *au* nerve to paired eye; *bg.* suboesophageal ganglion, consisting of several fused neuromeres; *cj* commissural ganglion; *g* brain; *go* optic ganglion; *m* (in *F*) stomach; *md* mandibular ganglion; *mx₁* and *mx₂* ganglia of first and second maxillae; *s* visceral nervous system; *sc* oesophageal commissure; *sg* (in *F*) visceral ganglion, *ua* nerve to median eye; *y* post-oesophageal commissure (? of ganglia of 2nd antennae). I–VIII thoracic ganglia; 1–6 abdominal ganglia. (From Lang.)

two lateral, closely aggregated together and each with a pigment mass in relation with it. In the Corycaeidae large dorsal cuticular lenses are developed * in relation with the paired lateral elements of the eye; but our knowledge of the morphology of the median eye is very defective.

The structure of the **paired eyes** has been already described (p. 329). In many Branchiopoda they sink into the body and are covered by a fold of the epidermis (Grobben).

The nature of the paired eyes.—The morphological nature of the compound eyes of Crustacea has been much discussed, and the evidence still appears to be conflicting. In the Decapoda and other groups of higher Crustacea they are mounted on jointed stalks and have therefore, to this extent, the character of limbs. As has recently been clearly shown by Herbst,† they may be replaced after injury by an antenna-like appendage. On these grounds it has been urged that the crustacean paired eye is, in fact, the modified appendage of the first segment of the head.

On the other hand the eyes are sessile in Trilobites, an ancient and apparently primitive form of the crustacean stock. The compound eyes of Insects have a similar structure to those of the Crustacea and they are apparently derived from the groups of simple ocelli such as we meet with in the Myriapoda, and the Collembola. If these are to be regarded as limbs they represent the arthropod appendage in an extreme modification indeed. Moreover the preantennary segment, of which the protocerebrum is the neuromere, bears a vestigial appendage in the embryo of *Scolopendra* (Fig. 229, 1).

The argument for regarding the paired crustacean eye as a modified limb, which appears at first sight to be most cogent, is that emphasized by the experiments of Herbst. The phenomenon is apparently allied to that of homeösis.‡ In the same way, to take one of many instances, the first antenna of an *Asellus* may, as an individual variation, assume the character of a mandible. The force of this evidence in its bearing on the appendicular nature of the crustacean eye depends on the extent to which homeösis is confined to truly homologous parts. The apparently analogous case, quoted by Bateson (l.c. p. 148), in which the hind leg

* Hartog shows that these are present also, though small, in relation with the lateral elements of the eye of *Cyclops*.

† *Archiv. f. Entwicklungsmechanik d. Organismen*, vols. 2, 9 and 13.

‡ Bateson, *Materials for the Study of Variation*, p. 84. Homeösis is defined as "the assumption by one member of a meristic series of the form or characters proper to other members of the series."

of a Burnet Moth is represented by a hind wing appears to show that it is not always so confined. In view of such a case can it be assumed that a lobe of the head not originally a limb, but lying in the line of the limbs, cannot take on the character of a limb? The amount of weight which we allow to the results of Herbst's experiments in their bearing on the appendicular nature of the paired eyes depends on the answer to this question.

Vesicular sense organs, usually opening to the exterior and containing delicate sensory hairs and hard particles, are found in the basal segment of the first antenna in many Decapods, and closed vesicles of similar structure occur in the uropods of the Mysidae. The open sacks contain sand, which is renewed at each ecdysis. The closed vesicles are said to contain concretions of calcium fluoride. It has been generally assumed that these are auditory organs; * but Kreidl † has shown, by an ingenious experiment, that they have another function. Specimens of the prawns *Palaemon xiphius* and *P. squilla*, shortly before an ecdysis, were kept in an aquarium in which sand at the bottom was replaced by iron in a state of fine subdivision. At the ecdysis the lining of the sack of the sense organ was shed, with the rest of the outer cuticle, and the sack was furnished afresh by the *Palaemon* from the materials available, namely iron particles. On bringing a magnet into its neighbourhood the *Palaemon* was now found to incline the body, so that the median plane was directed obliquely according as the particles were attracted to one side or the other of the sack, and gave rise to a corresponding stimulus to the hairs in it. It was thus apparent that a function of the sack was to inform the animal, normally by the action of gravity on the contained particles, of its relations in space. Delage ‡ has come to similar conclusions on the function of the organs in the tail of Mysidae.

Beer § concludes that all the organs, generally regarded until lately as otocysts in the Crustacea, are in reality of similar function, i.e. that they are not auditory but, to use Verworn's name, *statocysts*. It would appear however, from the possession

* Cf. Hensen, Studien üb. d. Gehörorgan der Decapoden, *Zeit. f. wis. Zool.* Bd. 13, 1863.

† Physiologie der Ohr-labyrinth, *Sitz. Ber. Akad. Wien.*, Bd. 102, Abth. 3, p. 149.

‡ *Comptes Rendus*, T. 103 (1886).

§ Statocysten-function, *Arch. f. ges. Physiologie*, Bd. 73 (1898).

of a stridulating apparatus by some Decapoda (Ocypod Crabs and the Hermit Crabs *Coenobita*), which live largely in air,* that a corresponding auditory organ must be present somewhere in the body; and the possibility is not excluded that the sacks in question have, as in Vertebrata, a double function, informing their owner of the presence of audible vibrations, and also of their own relation in space.

The alimentary canal consists of fore- mid- and hind-guts, of which the first and last are lined by chitin and derived respectively from the stomodaeal and proctodaeal involutions (ectodermal) of the embryo, while the mid-gut is endodermal. The remarkably small extent of the mid-gut in the Isopoda and some Decapoda, and the corresponding increase in length of the hind-gut have been already mentioned (p. 340).

The fore-gut is usually a short and simple tube in the Entomostraca, but in most Malacostraca its posterior region is modified into the masticatory stomach. Salivary glands are usually wanting. From the upper end of the oesophagus the alimentary canal usually runs straight to its termination, though it is coiled in some Cladocera, and Calman finds that the Cumacean *Platycuma Holti* has a tract of the gut (? fore-gut) coiled. The mid-gut is marked off by constrictions anteriorly and posteriorly; in front it is produced into diverticula, which are usually called the *liver*, but as their walls contain ferment cells the term *hepatopancreas* probably more nearly expresses their function. They may be paired (Fig. 251) or unpaired in the Entomostraca, and in the Malacostraca are represented by one to four pairs and they may remain simple, or be subdivided as in Decapods. In Stomatopods it has recently been shown by Orlandi † that there are two of these diverticula opening into the anterior part of the mid-gut, lying parallel with the alimentary canal, and expanding into voluminous lateral branches in the posterior segments of the body including the telson. The supposed segmental and hence exceptional relation of these branches with the gut in this group is thus shown not to exist.

In some Amphipods a single or paired caecum is present at the

* Cf. Alcock, *Ann. and Mag. of Nat. Hist.*, ser. 6, vol. 10, p. 336.

† S. Orlandi, Sulla Struttura dell' intestino della *Squilla mantis* Rond., *Atti della Soc. Ligustica di Sc. nat. e geog.*, vol. xii. N. 2 (1901), p. 112.

posterior end of the mid-gut, but the excretory function attributed to it is doubtful. In any case it is not comparable with the malpighian tubes of Insects, which are diverticula of the hind-gut. The hind-gut in Crustacea is without appendages.

The peristaltic contractions of the gut subserve the circulation of the blood, and it appears to be the chief agent for this purpose in the small Entomostraca which are without a heart.

The chitinous linings of the fore- and hind-guts are shed at each ecdysis. The remarkable paired calcareous concretions, known as **crabs' eyes** and found in the walls of the stomach of Decapods are also shed at this time and, being ground up by the stomach, apparently furnish the lime salts for the hardening of the new external cuticle.

In the strangely distorted and blood-sucking females of some parasitic Isopods (Epicarida) the alimentary canal ends blindly, as it does in some aberrant Cirripedes. In the Rhizocephala and adult Monstrillidae the canal is absent altogether.

The **blood** of *Astacus* and of other Decapod Crustacea and of *Squilla* is a clear fluid containing *haemocyanin*, a respiratory substance in which copper is present in combination with a proteid. It is colourless when deoxidized, but bright blue when oxidized (oxyhaemocyanin). A red substance may also be present—"tetronerythrin"—but it is doubtful if the latter possesses a respiratory function. In the Branchiopods *Daphnia* and *Chirocephalus*, however, Lankester found that the respiratory substance of the blood plasma is *haemoglobin*, and this is the case also in *Apus*, *Cypris*, and in the parasitic Copepod *Lernanthropus*.* Floating in the plasma are colourless amoeboid corpuscles.

The Crustacean circulatory system consists of a heart (absent however in the Cirripedes and many Ostracods and Copepods) lying dorsal to the alimentary canal, a system of arterial vessels more or less extensive, and of the lacunar haemocoel, of which the pericardium is part.

The Phyllopod *Branchipus* (Fig. 247) possesses a condition of the circulatory system, which may well be regarded as primitive. The heart is a long vessel traversing the thorax and abdomen, and provided with a pair of valvular *ostia* in each

* Cf. Halliburton, Blood of Decapoda, *Journ. of Physiology*, vol. vi. 1885.

segment, through which the blood enters from the surrounding pericardium. A terminal ostium is situated at the posterior end of the heart and the blood is propelled forwards by rhythmic contractions. The "aortic" artery leading forwards from the anterior end opens into the system of lacunae which pervades the body, especially the superficial regions beneath the integument. In the limbs the lacunae are so arranged that the blood flows down one side and up the other, supplying the epipodial branchiae in its course. An incomplete transverse septum dorsal to the alimentary canal separates the pericardial sinus from the lacunae ventral to it.

The variants on this arrangement met with in other groups of Crustacea consist mainly in the shortening of the heart and pericardium in various degrees (until we reach the capsular form of heart found in the Euphausiidae and Decapods on the one hand, and the Cladocera on the other) and in the development of the system of arteries between the heart and haemocoel. This system is most complete in the Decapods where the trunks become subdivided into arterial capillaries. A remarkable vessel found in this group, and in the Schizopods and Stomatopods is the **sternal artery** which passes ventrally from the heart on one side of the intestine and between the parallel strands of the nerve cord to communicate with the subneural artery from which the limbs are supplied.

In Decapods the gills are supplied by a system of lacunae independent of the vessels to the limbs, an afferent set leading from the large cephalo-thoracic sinus to the gills, and an efferent conducting the blood to the pericardium, where it mixes with the venous blood returned from other parts. In this group the blood is propelled backwards as well as forwards, a superior abdominal artery extending backwards from the heart above the intestine. As the heart is abbreviated in the several groups the number of ostia diminishes.

The **excretory organs** usually consist of a more or less coiled tube ending internally in a sack and opening at the base of an appendage. They are probably homologous with the segmental tubes of Annelida and other coelomate animals. In the Malacostraca the *antennal gland* (the *green gland of Astacus*) opening at the base of the second antenna is usually the excretory organ of adult life, though the *maxillary gland* is found in the

larva (and, in Cumacea, and Stomatopods in the adult). In the Entomostraca the latter is usually the functional gland in the adult. It opens at the base of the second maxilla, and is frequently contained in the fold of the shell, and hence known as the *shell gland*.

Reproductive Organs. The sexes are distinct in the great majority of the Crustacea. The Cirripedia, however, which lose their locomotive powers early in larval life and become attached, are in nearly all cases hermaphrodite, thus offering a parallel with many, though by no means all, other sessile animals (Tunicata, *Phoronis*, many Polyzoa). Among Cirripedes also occurs (*Scalpellum*, *Ibla*) a remarkable form of dimorphism, the association of supplemental and degenerate dwarf males with the hermaphrodite individuals (p. 424). Several genera of the parasitic Cymothoidae and Epicaridea (Isopoda) are also hermaphrodite, and protandrous, i.e. a male phase precedes the female phase in the life of the individual (p. 484). The remarkable tendency to a hermaphrodite condition in male Decapods, when they recover from the suppression of the reproductive organs induced by cirripede and other parasites is alluded to below (p. 445).

The reproductive organs are formed on the same type in the two sexes, and usually occupy similar positions, dorsal to the intestine. In both they consist of a single pair of gonads with the corresponding ducts, though fusion to a greater or less extent between those of opposite sides may occur. The ducts (mesodermal) are continuous with the gonads, and meet distally an invaginated ectodermal tract opening to the exterior.

In *Cyclops* the rudiments of the gonad ("stem-cell") can be distinguished at an early stage of segmentation.

The *spermatozoa* vary widely in character. They are amoeboid in *Polyphemus* (Cladocera), oval or sausage-shaped in the Copepods, spherical and beset with stiff radial processes in some Decapods, Euphausiidae and Stomatopods. They are often filiform (though not always, e.g. *Danalia*) in Isopods and Amphipods, in the Cirripedes, and the Ostracods, in which latter group they are of gigantic size (up to 10 lines), exceeding the whole body in length three or four times. In many cases they are apparently not mobile, but it is not the case, as sometimes

stated, that they are always motionless in Crustacea ; for those of *Polyphemus*, Cirripedes and Ostracods have been observed actively mobile. The non-mobile condition finds a parallel in the Chilognatha and in some Arachnids. In Decapods fertilisation is effected, according to Koltzoff, by the action of an explosive capsule which is carried by the spermatozoon (cf. p. 525).

In many groups of Crustacea the spermatozoa are encased in *spermatophores*, secreted by the terminal portions of the male ducts.

The remarkable manner in which the eggs of the Cladocera are nourished at the expense of neighbouring germ cells is alluded to in the description of that group (p. 379).

In the Entomostraca the genital ducts of both sexes usually terminate at a segment lying at the limit between thorax and abdomen whatever the numerical position of this segment may be ; though the Cirripedes are exceptional in that the oviducts open on the basal segment of the first thoracic appendage. In the Malacostraca the positions of the genital openings are fixed, like the number of the segments, the oviducts opening on the 6th, the vasa deferentia on the 8th thoracic segment, either on the base of the appendage or near by on the sternum. It follows, on the view that the genital ducts are derived from segmental organs, that in the Malacostraca the segmental organs of different segments subserve the transmission of the reproductive products in the two sexes:

In many Copepods paired or single sperm passages are found in the female leading to the receptaculum seminis and distinct from the direct orifices of the oviducts. To these openings (or opening) the spermatophores are attached by the male. The remarkable birth-aperture described by Schöbl in woodlice is referred to in the section dealing with the Isopoda (p. 483).

The **secondary sexual characters** in the shape of sense organs and prehensile modifications of the limbs, together with the many remarkable forms of **sexual dimorphism** found among the Crustacea are described under the several subdivisions.

Larval histories. One of the most interesting features of the Crustacea is the occurrence in all the chief groups, however diverse the forms of the adult may be, of a larva with certain constant characters, the *Nauplius* (Fig. 242). The name was originally given by O. F. Müller towards the end of the

eighteenth century to an early stage in the development of *Cyclops*, under the supposition that it represented a distinct generic type. It is now used for a larva, to whatever group of Crustacea it may belong, having the following characters.

The body is oval in shape, wider in front than behind, and shows no trace of external segmentation. A dorsal shield is usually absent, though it occurs in the nauplius of some Cirripedes and of the Cypridae (Ostracoda) (Fig. 256). A pair of setae projects on either side of the hind end. Three pairs of appendages are

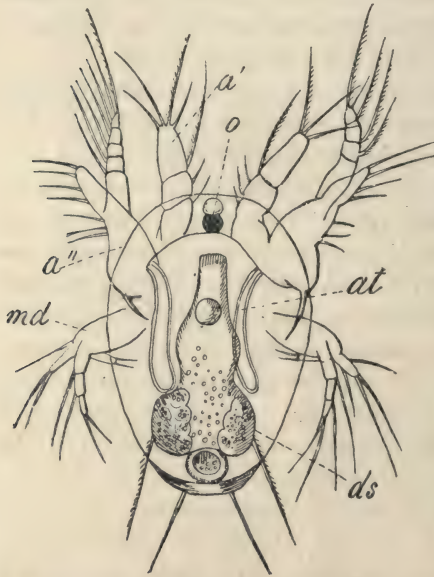


FIG. 242.—Nauplius of *Cyclops*, dorsal aspect (from Korschelt and Heider, after Claus). *a'* first antenna; *a''* second antenna; *at* antennal gland; *ds* mid-gut with excretory cells; *md* mandible; *o* median eye.

borne by the nauplius larva; the anterior (Fig. 242, *a'*) the 1st antennae of the adult, and placed in front of the mouth, being unbranched, while the two posterior, which become the 2nd antennae and mandibles, are biramous and paroral and postoral respectively. The 2nd antennae carry a masticatory endite directed inwards and acting as a jaw, but the mandibles are, as yet, usually without such a process. A large upper lip projects in front of the mouth, and the alimentary canal presents a division into oeso-

phagus, mid- and hind-gut, though the anus is not always open on hatching. The innervation of the 2nd antennae is from a postoral pair of ganglia, as in some adult Branchiopods. The unpaired median eye is the sole organ of vision, and a heart is not yet formed. The little larva moves rapidly through the water, by the strokes of all three pairs of limbs.

When it is recognized that a nauplius stage occurs in the development of the free-swimming Copepods and of their un-gainly parastic relations, in the Barnacles and *Sacculina*, in

Cypris, *Apus*, *Branchipus* and *Leptodora* (winter eggs); and among the Malacostraca in *Euphausia*, *Leucifer* and *Penaeus* it is astonishing what diverse forms are knit together by this three-limbed larva. In all these the young enter on a free life as soon as they are hatched, and the adult form is attained in a series of moults by a more or less gradual metamorphosis. But in other cases, as in the Cladocera, many Ostracods, *Nebalia* and the "Peracarida" the young are protected, in one way or another, during their development, by the mother, and the metamorphosis is greatly abbreviated. Nevertheless some indication of the 3-limbed nauplius stage, and the throwing off of a nauplius skin occur in all.

In the Entomostraca with free swimming larvae the advance to the adult state is by a series of gradual changes, but in the Malacostraca a number of remarkable larval forms are found, belonging to stages which succeed the nauplius, and adapted to a pelagic existence (p. 448 ff).

In most, though not in all, cases (and markedly not in the Zoea larva) the segments and appendages appear in order from before backwards, the former being differentiated from a budding zone at the posterior end of the larva.

Various contrivances are found among the Crustacea for the protection of the eggs and of the young. In several groups the batch of eggs is contained in a sack formed by the hardened secretion of the oviduct. This may project freely as in the Copepods, and some Euphausiidae, or lie in the space between the dorsal shield and the body as in Cirripedes. In the Cladocera many Ostracods and *Estheria* the eggs lie free in this space and the whole of the development may occur in it. When the slowly-developing winter eggs of the Cladocera are produced the walls of the dorsal shield about them become thick and hard, forming the saddle-like "*ephippium*," which being shed at the next moult with the eggs contained in it, forms a bivalved case for their protection. In the Apodidae two lobes of one appendage become opposed to form the egg case on either side. In many Malacostraca a brood pouch is formed as we have seen by the modification of epipodites of some of the thoracic limbs into oostegites, and between them and the ventral surface of the mother the young are protected. In the Decapoda the eggs are attached by a sticky secretion to the long setae on the

abdominal legs of the female (many *Macrura*) or enclosed between the flexed abdomen and the thorax.

Fossil forms. The differentiation of the main types of Crustacea had occurred before the palaeontological record begins. The Carboniferous rocks contain examples of four out of the five Entomostracan orders, the Branchiopods being represented among other forms by *Estheria*, a genus which has existed from the Devonian period to the present day, the Cirripedes by *Pollicipes* and *Scalpellum*, which go back to the Ordovician, and the Ostracods by a variety of genera which already peopled the Cambrian waters, the genera *Cythere* and *Bairdia* extending from the Ordovician to the present day. The fourth order, the Trilobites, is well established in the Cambrian rocks, attains its highest development in the Ordovician and by Devonian times was already on the wane. It is doubtful if they extended beyond the Carboniferous period. The remaining Entomostracan order, the Copepods, consisting of small and thin-shelled forms, have not been recognized in any geological formation.

A number of genera found in the Palaeozoic rocks from the Cambrian to the Carboniferous appear to be related to the most primitive group of the Malacostraca—*Nebalia* and its allies. Among these may be mentioned *Ceratiocaris* (Cambrian to Carboniferous) and *Hymenocaris* (Cambrian), *Echinocaris* (Devonian) and *Dithyrocaris* (Carboniferous). They have thin bivalved or at least bilobed shells and the abdomen is apparently without appendages though ending in a well-marked caudal fork. They have been referred by many authors to the Phyllopods, but the presence in *Ceratiocaris* of a rostral plate appears to justify the association of this genus at least with *Nebalia*.

The Carboniferous genera *Palaeocaris* and *Acanthotelson* and the Permian *Gampsonyx* and *Nectotelson* (Brocchi) and perhaps also *Gasocaris* (Fritsch) find their ally, as was first ably shown by Calman, in the existing Tasmanian genus *Anaspides*, and form, with it, the group of the Syncarida (Packard).

The caridoid type of Malacostraca—shrimp-like forms with dorsal shield, well-developed swimming abdomen ending in a caudal fin, stalked eyes and a scale-like exopodite to the 2nd antenna—is represented in the Carboniferous rocks by a number of well-preserved fossils:—*Palaeopalaemon* Whitfield, appearing in the Devonian, *Crangopsis* (*Palaeocrangon*) and *Anthrapalae-*

mon Salter. Whether these are to be regarded as true Decapods or as belonging to either of the groups of Schizopods is an open question, as is, indeed, the case with regard to some existing species. *Pygocephalus*, from the Coal Measures, appears to be a true Schizopod, belonging to the division of the order classed with the Peracarida.* Clearly marked *Macrura* appear in the Trias and are well represented in Jurassic rocks. The first undoubted *Anomura* and *Brachyura* occur in Cretaceous strata, though *Palaeinachus* has fair claims to represent the latter suborder in the Jurassic period.

Sculda (Jurassic) and *Squilla* (Cretaceous) give the first clear evidence of the Stomatopods.

Cyclosphaeroma from the Great Oolite is undoubtedly an Isopod, but it is far from certain that we possess any earlier representatives of the order. It is interesting to recognize the characteristic tumours caused by parasitic (Bopyroid ?) Isopods in the fossil crabs (*Palaeocorystes*) of the Cambridge Greensand.

The first unquestionable Amphipod is not met with until the Tertiary (Miocene) strata, though a number of obscure Palaeozoic forms have been referred to this order. No fossil Cumacea have been recognized.†

On reviewing the palaeontological history of the several orders of Crustacea, the Entomostraca appear to have been differentiated at a period before the record begins, and four of their five orders were well established together with certain main types of the Malacostraca (Leptostraca, Syncarida and the Caridoid type) by the Carboniferous period. It may however fairly be claimed that the order of appearance of the subdivisions of the Malacostraca is consistent with the conclusions as to their relationship to which we are led on purely morphological grounds.

Sub-class 1. ENTOMOSTRACA.

The name Entomostraca, though established by long usage, is without etymological significance as contrasted with that of

* Cf. H. Woodward on the genus *Pygocephalus* Huxley, a primitive Schizopod Crustacean, from the Coal Measures. *Geol. Magazine*, decade 5, vol. iv, p. 339, Sept. 1907.

† The author desires to express his indebtedness to Mr. H. Woods of St. John's College, Cambridge, for his assistance in preparing this notice of the palaeontological record of the Crustacea.

the other great division of the Crustacea, the Malacostraca.* This latter was applied by Aristotle to crabs, lobsters and other members of the higher Decapoda, and found its application in contrast, not with the Entomostraca, which were probably unknown to Aristotle, but with a group of "shell-fish" with a still harder shell—the oysters, and other bivalves.

Aristotle's ζῶα ἐντομα † included insects, arachnids, myriapods and apparently the land isopods, as well as annelids. Writers of the 18th and early 19th centuries used the name Crustacea for Aristotle's Malacostraca, and the name Entomostraca (first employed by O. F. Müller, 1785) was applied, though without very direct antithesis, to a group of animals regarded as distinct from the Crustacea, as thus understood, and approximating more nearly to insects. Even so late as 1840, Erichson distinguished between Entomostraca and Crustacea and included in the former *Limulus*, together with *Apus*, *Branchipus*, *Daphnia*, *Cypris*, the Cirripedes, *Cyclops*, *Lernaea*, etc. Some time before this date, however, many naturalists had recognised the necessity of establishing a comprehensive group to which the name Crustacea was applied. Aristotle's name Malacostraca was revived to designate, though in a larger sense, the higher division of Crustacea, while that of Entomostraca was employed for the lower division, with the exclusion of *Limulus*. It has thus come about that the names Entomostraca and Malacostraca stand for the two divisions of the Crustacea, though the members of the former group are not more conspicuously segmented than those of the latter, and the Malacostraca have as a whole firmer shells than the Entomostraca.

There are not many positive characters which distinguish the Entomostraca as a group. They are for the most part animals of small size as compared with the Malacostraca. The number of body segments, though fixed in Cirripedes and approximately constant in Copepods, varies widely in the other orders. The abdomen commonly terminates in a caudal fork. The excretory glands of both second antennary and second maxillary segments are developed in the course of the life-history, but it is the latter which (as the "shell-gland" in some groups) becomes the excretory organ of the adult—a relation the reverse of that usually

* μάλακός soft. ὀστρακον shell.

† ζῶον a living thing; ἐντομος cut in pieces, or, as we say, "segmented."

obtaining in the Malacostraca.* The median eye of the larva nearly always persists, though often with compound lateral eyes in addition. The stomach is usually without a masticatory apparatus, though a regular "mill" is present in some Ostracods, notably in *Bairdia*. The ganglion of the second antennary segment retains its suboesophageal position at any rate in two divisions of the Branchiopods. Among Phyllopods also we find a very simple condition of the heart, it being (in *Branchipus*) a uniform tube with a pair of ostia corresponding to each of the segments in which it lies.

On the whole the Entomostraca are distinguished by a simple and apparently more primitive grade of organization than is found in the Malacostraca, and also by the absence of those characters by the possession of which the Malacostraca are united. They are however a much less homogeneous group than the latter, and it is the fact that most divisions of the Entomostraca differ more from one another than *Nebalia* does from some members of the Phyllopoda.

Each group which has left any palaeontological record at all was already well differentiated by the Ordovician period. The Trilobites died out early, but certain genera of the Branchiopoda, Ostracoda and Cirripedia have persisted from Ordovician times to the present day.

Order 1. TRILOBITA.†

Palaeozoic Crustacea with one pair of antennae and (apparently) four other pairs of cephalic appendages, the gnathobases of the latter serving as jaws. Of the numerous (up to 30) segments of the trunk the anterior are free and the posterior are united into a pygidium. All the trunk segments except the last (telson) bear biramous appendages.

* In the Ostracoda (*Cypris*) however both antennary and maxillary glands are found by Claus to be present in the adult.

† Burmeister, *Die Organisation der Trilobiten*, etc., Berlin, 1843. Beyrich, *Unters. üb. Trilobiten*, Berlin, 1845, 1846. Barrande, *Système silurien du centre de la Bohême*, Prague, 1852. Salter, S. W., *A monograph of the British Trilobites*, London, 1864-1866. Walcott, C. D., *Fossils of the Utica Slate*, *Trans. Albany Inst.*, vol. X, 1883 (separate copies 1879). Id., Note on some appendages of Trilobites, *Proc. Biol. Soc. Washington*, vol. 9. Beecher, C. E., Several papers (in *American Journ. of Sc.*, ser. III, vol. 46 and 47, and in *American Geologist*, vols. 13, 15 and 16), collected in *Studies in Evolution*, Yale Univ. Publ., London, 1901.

Trilobites abound in Cambrian and Silurian strata in many parts of the world, but appear not to have survived to the secondary period. Though the preservation of the head and trunk is often as perfect as can be desired no traces of appendages were for a long time found, but within the last few years the Utica shales (Lower Silurian) of the State of New York have yielded abundant examples of a trilobite, *Triarthrus Becki*, the organic parts of which are replaced by iron pyrites. These

have been made the subject of a series of reports by Beecher. Many features of the appendages of these specimens are preserved in minute detail, and their discovery has put our knowledge of the group on a new level. Unfortunately, however, notwithstanding the care which has been devoted to their elucidation, we are still left in tantalizing uncertainty on several points.

The body of Trilobites is oval, and dorso-ventrally flattened. It consists of a head and of a segmented trunk the anterior somites of which were movable on one another, while the posterior are united, as in many Isopoda, to form the *pygidium*; and, like woodlice, the animals possessed the power

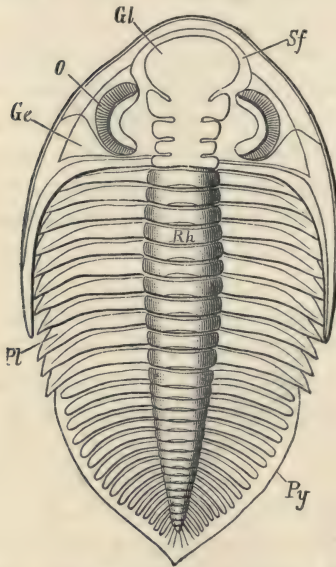


FIG. 243.—Diagram of *Dalmanites*. *Ge* gena; *Gl* glabella; *O* eye; *Pl* pleuron; *Py* pygidium; *Rh* rhachis; *Sf* facial or ocular suture (the leader extends a little beyond the suture). From Claus, after Pictet.

of rolling themselves into a ball, in which position they are often preserved.

In both head and trunk a central part is divided by longitudinal grooves from pleural regions, causing the tripartite division of the body in allusion to which the group was named.

On the central part of the head, known as the *glabella*, transverse grooves usually indicate a division into five segments, of which the posterior or *occipital* segment is most distinct (Fig. 244). The anterior and lateral regions of the head end in a sharp

border, and the postero-lateral angles are often produced into long backward-directed processes.

The pleural regions of the head are known as the *genae* or cheeks, and bear the large reniform, many-faceted *eyes* which are in some cases raised on prominences of the head shield. In *Harpes* the eyes are replaced by groups of two or three ocelli, and in some genera they were absent altogether. The gena of either side is traversed by the *facial* or *ocular suture*, which runs forwards from the hinder or outer margin, passing on the median side of the eye, and is continuous with its fellow in the middle line in front of the glabella.

From the fact that in decayed specimens the regions of the head fall apart at this suture it is conjectured that some small amount of movement between the head regions may have been admitted during life and the terms "fixed" and "movable cheeks" have been applied to the areas of the genae internal and external to the ocular suture.

In addition to the eyes on the upper surface of the head, some trilobites possess structures on the under surface which are also, apparently, eyes. They are situated on either side of the posterior third of the hypostome. Each consists of a small oval area, called a *macula* by Lindström. In some genera they are smooth; in others they are partly or entirely faceted, and resemble in structure the dorsal eyes.*

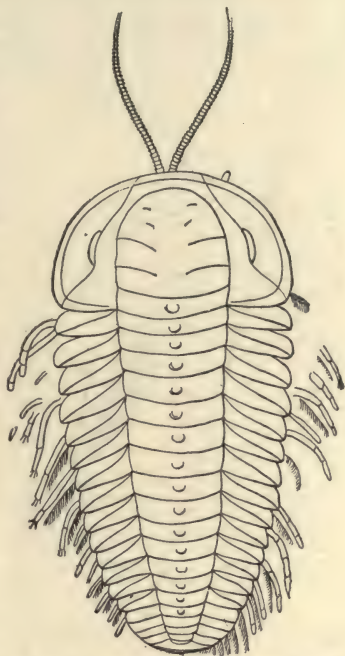


FIG. 244.—Dorsal surface of *Triarthrus Becki*. After Beecher.

The free trunk-segments vary in number from two (*Agnostus*) to twenty-nine. Those of the pygidium also vary in different genera (from 2–28, though the number is by no means complementary to that of the free segments), as does the completeness of their fusion into a uniform plate.

The terminal segment (telson) is without appendages and the anus is situated on its under surface. The sternal region of

* G. Lindström, Researches on the Visual Organs of Trilobites, Kongl. Svenska Vetenskaps Akad. Bandet 34, 1901.

the trunk segments is sometimes traversed by longitudinal oblique ridges, interpreted by Beecher as marking the apodemes for muscular insertion.

Beneath the head a large labrum (*hypostoma*) projects back over the mouth, and a small lower lip is placed behind it.

Appendages. A pair of long annulated antennae (Fig. 244), with a large basal joint, are inserted on either side of the labrum.

From the region of the mouth a series of appendages, set wide apart, at the ends of broad sternites, extends to the end of the pygidium. In the post-cephalic region they have, in *Triarthrus*, the following characters. They are biramous but peculiar among crustacean limbs in being deeply cleft down to the coxal process (Fig. 245). The endopodite is cylindrical in

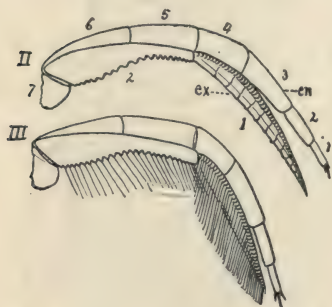


FIG. 245. — Dorsal view of the right second and third thoracic legs of *Triarthrus*, as restored by Beecher. In II. the setae are omitted. *en* endopodite, with segments 1-6; *ex* exopodite, with segments 1-2. 7 the problematical coxal process or gnathobase.

the anterior part of the trunk, but its basal segments become more and more lamellar as the series is followed back. The exopodite consists of a long basal segment and a multiarticulate terminal portion, both beset with an abundant fringe of long setae. From the base of the limb what appears to be a coxal endite extends inwards towards its fellow, as in *Apus* and its allies; but as, apart from this, it is not clear that there is any uncleft basal portion of the limb (protopo-

dite), the homology of this element of the limb remains for the present obscure.

In the head Beecher concluded that there were four pairs of appendages in addition to the antennae, though, owing to the difficulty in determining their points of insertion, the number assigned to the head is in part a deduction from the number of the segmental grooves on the dorsal surface of the glabella.

The two posterior head appendages appear to have had a structure similar to that of the legs behind them, though with a longer and denticulated gnathobase. The two appendages in front of them had also, apparently, a large gnathobase, but the conclusion that their appendages, like those of the segments

behind them, were also biramous appears to rest on insecure foundation.

The Utica shales have also yielded specimens of *Trinucleus* in which the pygidial appendages are displayed, and these resemble the corresponding structures in *Triarthrus*, though considerably shorter.

Before the discovery of this material much light was thrown on the nature of the appendages of Trilobites by Walcott who examined a large number of fossils of *Calymene* by means of sections. He concluded that two long and sometimes spirally twisted epipodial lobes were appended to the outer side of the base of the biramous limb. In view of the difficulty of arriving at certain results by this method, and of the fact that *Triarthrus* yields no trace of such structures, their existence in *Calymene* appears very doubtful.

Development. Remains of young trilobites are sometimes found associated with those of adults, and the successive stages of the development of the head and trunk have been traced by Barrande and by Beecher. In the earliest which has been recognized, the *protaspis* stage of the latter author, they are minute oval bodies 4-1 mm. in length, with indications of the five divisions of the glabella, and of one succeeding segment. The eyes are anterior and marginal when they first appear, the subsequent change in position causing the indentation of the ocular suture of the adult. The appendages of the young have not been seen.



FIG. 246.—Larva of *Dalmanites socialis* Bar. in the "ana-protaspis" stage. A pygidium of three segments is present, but there are as yet no free thoracic segments. $\times 30$. From Beecher, after Barrande.

The fact, pointed out by Barrande, that in *Trinucleus*, and other genera a pygidium is formed before the number of free thoracic segments is complete, does not, as might at first appear, necessarily show that the region of the formation of fresh segments was in front of the pygidium. We are at liberty to suppose that the formation of fresh segments occurred at the posterior end of the body, as in most other young Crustacea, and that segments which at one stage of growth belonged to the pygidium became in a later stage, after casting a shell, free thoracic segments.

Occurrence. The remains of Trilobites are associated in marine strata with those of Crinoids, Brachiopods and Cephalopods. The absence of eyes in some cases is perhaps an indication that the species so characterized inhabited deep water.

In view of the high interest attaching to Trilobites as ancient

and primitive members of the Crustacean series, it is most undesirable to press the evidence for more than it is worth; and in the foregoing account of the appendages an attempt has been made to show where, as appears from the published descriptions, the ground is still insecure. It seems certain that they possessed only one pair of antennae, and, taking into account the indications of segmentation in the glabella of the larva and of the adult in addition to the evidence afforded by the appendages, the existence of four other cephalic limbs, provided with gnathobases, appears probable. The establishment of these results would confirm in the most striking manner the conclusions which have been arrived at from the study of the existing fauna on the nature of the second antennae of Crustacea—namely that they are postoral appendages, which have in recent forms become preoral.

Besides the characters of the second cephalic limbs and the indication of segmentation of the glabella into five segments, we may recognize as primitive features the presence of limbs on all the segments except the telson, the varying and usually large number of the body segments and the small degree of specialization in the series of appendages, though how far this applies to the head appendages must remain for the present undecided.

In the two last features Trilobites resemble the Phyllopods among the Branchiopoda, to which group Burmeister had pointed out their resemblance before the discovery of the appendages. It is also shown in the large hypostoma and the gnathobases of the post-cephalic limbs; and the absence of a carapace finds a parallel in *Branchipus* and its allies. On the other hand the deeply cloven character of the limbs removes the Trilobites from the immediate neighbourhood of Phyllopods, as also from all other recent forms.

Until the appendages were discovered Trilobites were usually classed with *Limulus* and its allies, on account of the shape of the head shield, the position of the eyes and the so-called "trilobite stage" in the development of *Limulus*. This association is indeed still retained by many authors, but the indication of five pairs of cephalic appendages, as in the Crustacea, not seven as in the cephalo-thorax of the Merostomata, and the evidence which we now have on the

characters of the appendages, the antennae and the others, appear to remove them widely from the latter group and to bear indisputable testimony to their Crustacean affinity.

Order 2. BRANCHIOPODA.*

Crustacea with an elongated and often distinctly segmented body; usually with a flat shield-like carapace or laterally compressed bivalve shell, formed by a reduplication of the skin. The mandible is without a palp in the adult. There are at least four and generally many pairs of swimming feet, which are in nearly all cases leaf-like and lobed.

The animals belonging to this order differ very considerably in form and size, in the number of their segments and appendages, as well as in their internal anatomy. They agree however in the lobed and leaf-like character of their feet. Of the two groups into which they are divided, the Phyllopoda are probably the most primitive form of Crustacea which has survived. Their primitive character is seen in the large and varying number of segments of the body, the small degree of differentiation throughout the series of their appendages, the tubular heart with the segmentally arranged ostia, the simple character of the ganglionic chain, and the persistence in all of them of the nauplius larva. The other group, the Cladocera, may be regarded as an off-set from this primitive stock (probably from a form allied to the Conchostraca) in which the number of appendages and the size of the body have been reduced and its segmentation obscured.

The body is either cylindrical, elongated and clearly seg-

* Besides the works of O. Fr. Müller, Jurine, M. Edwards and Dana compare Zaddach, *De apodis cancriformis anatome et historia evolutionis*, Bonnae, 1841. E. Grube, *Bemerkungen über die Phyllopoden*, *Arch. für Naturgeschichte*, 1853 and 1855. Fr. Leydig, *Monographie der Daphniden*, Tübingen, 1860. C. Claus, *Zur Kenntniss d. Baues u. Entwickl. v. Branchipus u. Apus*, Göttingen, 1873. *Zur Kenntniss d. Organisation etc. der Daphniden*, *Zeit. f. wiss. Zool.* Bd. 27. *Zur Kenntniss d. Baues u. d. Organisation. der Polyphemiden*, *Denkschr. Akad. Wien, Math. Nat. Classe.* Bd. 37, 1887. Branchipus and Artemia, *Arch. Zool. Inst. Wien.* vi. A. Weismann, *Naturgesch. d. Daphnoiden*, Leipzig, 1876-79. Grobben, C., *Embryonalentwick. v. Moina rectirostris*, *Arch. Zool. Inst. Wien.* ii. Packard, *Monog. N. Amer. Phyllopod Crustacea*, Washington, 1883. P. Samassa, *Keimblätter-bildung bei Cladocera*, *Arch. f. mikr. Anat.*, Bd. 41. G. O. Sars, *Fauna Norvegiae*, Vol. 1, Phyllocarida and Phyllopoda, Christiania, 1896. M. T. Sudler, *Dev. Penilia*, *Pr. Boston Soc. N. H.*, Vol. 29, 1899, p. 109. Samter, *Entw. Leptodora*, *Zeit. f. wiss. Zool.* Bd. 68 (1900). Lilljeborg, *Cladocera Suecica*, *Nova Acta Soc. Sc. Upsala*, 1900.

mented, without free reduplication of the skin (*Branchipus*, Fig. 247), or it may be covered by a broad and flattened shield, an extension of the cephalic integument, which only allows the posterior part of the body to project uncovered (*Apus*, Fig. 248). In other cases the body is laterally compressed and enclosed

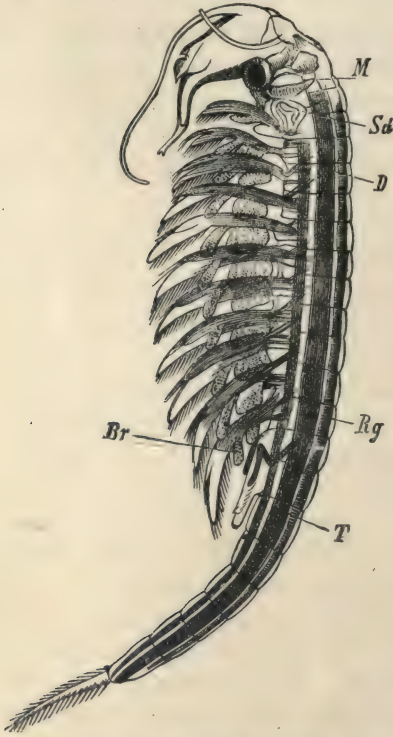


FIG. 247.—Male of *Branchipus stagnalis*. *Rg* heart or dorsal vessel with a pair of slit-like ostia in each segment; *D* intestine; *M* mandible; *Sd* shell gland; *Br* distal branchial appendages of the eleven pairs of legs; *T* testis. The anterior antenna is seen as a slender appendage curving forwards in front of the eye over the base of the strong, prehensile posterior antenna. The long tentacular and short foliaceous appendages of the latter are also seen.

by a bivalve shell from which the anterior part of the head projects (Cladocera) (Fig. 251); or finally the head together with the laterally compressed body is completely covered by a bivalve shell which is closed by a shell muscle passing between the valves (Conchostraca). Sometimes the head is sharply distinct from the rest of the body, and in one family, the Branchipodidae, the anterior part, bearing the eyes and antennae, is divided by a transverse groove from the posterior, bearing the other three pairs of cephalic appendages (Sars). As a rule the posterior segments only are without appendages. The hind end of the body is often curved forwards and may bear two rows of posteriorly directed claws, the last pair of which arise at the point of the tail, and are by far the strongest

(Cladocera). In other cases a pair of simple (*Branchipus*) or articulated (*Apus*) appendages are present, constituting the caudal fork.

Appendages. On the head there are two pairs of antennae, which however, in the adult animal, may be rudimentary or

peculiarly modified. The anterior antennae are small, and bear the delicate olfactory hairs. The posterior antennae frequently have the form of large biramous swimming appendages, but they may be modified as prehensile organs, e.g. in the males *Branchipus* and its allies (Fig. 247). In other cases (*Apus*) they are rudimentary (Fig. 248) and may even be entirely absent.

A pair of large mandibles is always present beneath the well developed upper lip; they possess a toothed, biting edge, and in the fully developed condition are destitute of palps.* The mandibles are followed by one or two pairs of slightly developed maxillae. A kind of underlip is in many cases present, in the form of a bilobed prominence behind the mandibles.

It is remarkable that while the thoracic appendages of the Branchiopods conform so uniformly to a common and, as it appears, primitive type of structure, the appendages about the mouth present the greatest divergence from that type which is met with in any group of Crustacea. The absence of the mandibular palp in the adult is all the more striking because of its size and frequently biramous character in other Entomostracan groups, the Copepods and Ostracods. Again, the two pairs of maxillae, which even in the Malacostraca conform more closely than any other appendage to the primitive "Phyllopod" type of limb, are here, in the Branchiopods themselves, perfectly simple lobes, and one pair is often missing. In adult Cladocera and in *Limnetis* among the Conchostraca there is only one pair, in *Branchipus* the second pair is rudimentary, and in this genus, as also in *Apus* where two pairs are present, they are retarded in development, appearing later than the thoracic appendages which follow them in position. It is interesting to note that in *Cypris*, among the Ostracods, the second maxillae are also retarded in their development. The late appearance of the maxillae is perhaps a confirmation of the view taken

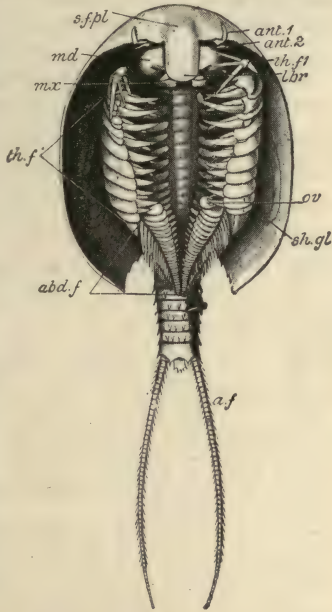


FIG. 248.—*Apus glacialis*, ventral aspect of female. *abd.f* abdominal limbs; *ant.1* first antenna; *ant.2* second antenna; *lbr* labrum; *md* mandible; *mx* first maxilla; *ov* brood pouch; *s.f.pl* sub-frontal plate; *sh.gl* shell-gland; *th.f* and *th.f* thoracic feet. (From Parker and Haswell, after Bernard.)

* Ekman finds a vestigial palp in *Polyartemia forcipata* (Bih. K. svenska vet Akad. Handlingar, Bd. 28 [1902]).

here, that the simple condition of these appendages in the Branchiopods is a specialized and not a primitive character. The small size and simple character of the maxillae is perhaps dependent on the peculiar habit of members of this genus, alluded to below, of passing the food forwards along the ventral groove.

The postcephalic appendages (*legs* or *feet*) are usually very numerous in the Branchiopoda Phyllopoda, and are smaller towards the posterior end of the body. In this division of the order they consist, as its name implies, of flattened leaf-like appendages which act as swimming feet, and by the eddies they set up in the water assist in procuring food. They are set transversely on either side of the ventral middle line, and the inner and outer margins are produced into endites and exites. In the mid-ventral line of the body, between the closely ranked legs of either side there is a deep groove, limited at the sides by the endites, and closed above by the sterna of the body segments. Along this groove the material containing the food is, in most if not all Branchiopods, passed forward to the mouth, assisted on its way by the movements of the appendages. It can thus be acted on by the opposed endites of the latter, set on either side. The basal endites, and especially the first or "coxal" endite, have accordingly the character of masticatory lobes, being short, firm and beset with coarse setae.

There are usually six endites on a leg (Fig. 249); those near the base directed inward, and those situated distally directed more and more in the line of the axis of the leg, so that the most distal form terminal lobes.

The exites are two or three in number. The most distal of them, having in several cases a triangular shape, is known as the *flabellum*. The proximal exite or exites (2 in *Polyartemia* and *Chirocephalus*) are generally simple lobes, devoid of setae.* A respiratory function has been especially attributed to them, but, as the justice of this is disputable, the term *bracts* may be conveniently retained for them.

It is not at all obvious how the short multilobed thoracic legs of the Branchiopoda conform to the biramous type of limb so widely found among the Crustacea; and, as a fact, now one and now another pair of the terminal lobes has been regarded

* In cases where two are present they appear to belong to the two proximal divisions of the protopodite.

by different authors as corresponding with the two branches usually met with. By a comparison of the undoubtedly biramous second antennae with the developing thoracic legs of the larval *Apus*, Lankester* has shown good reason for regarding the fifth and sixth (the two terminal) endites as the homologues of the endopodite and exopodite respectively. It follows that the *flabellum* must be regarded, not as an exopodite (its jointed flagellar termination in *Limnetis* notwithstanding) but as a distal epipodite.

In *Daphnia* among the Cladocera (Fig. 252) the epipodites are reduced to a single bract and the distal endites are diminished in size. The coxal endite on the other hand is large in the first pair of thoracic legs, and in the second and third pairs it forms a great comblike, backwardly directed plate.

In the Polyphemidae the anterior or all the legs have a cylindrical shape, and in *Leptodora* no epipodite is present.

It is remarkable that in *Apus*, which possesses a large number of appendages (40–63 pairs), while the anterior pairs correspond in number with the segments (as indicated by the annular constrictions and rings of cuticular spines on the surface of the body), being attached one to each, the posterior far outnumber the segments which bear them, so that one segment carries as many as five or six pairs of limbs.

The central nervous system is composed of a supra-oesophageal mass connected by commissures with a ventral chain of ganglia. The latter in the Phyllopoda presents nearly the same simple arrangement which is found in the Annelida, consisting of a pair of ganglia to each pair of appendages (Fig. 241, D). There are, however, in the Phyllopoda, two transverse commissures to each pair of ganglia. Even *Apus* with its large number of

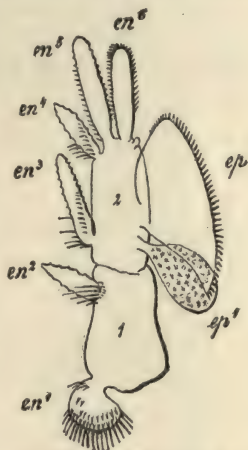


FIG. 249.—Second thoracic leg of *Apus cancriformis*. 1 first, 2 second stem joint; *En* 1–6 endites; *ep* flabellum; *ep'* bract (from Korschelt and Heider, after Lankester).

* *Q.J.M.S.*, vol. 21. The evidence here cited, and that brought forward by Thiele (Betrachtungen ü. die. Phylogenie der Crustaceenbeine. *Zeit. f. wiss. Zoologie*. Bd. 82 (1905) p. 445), who regards the flabellum as the exopodite, appear to be conflicting.

appendages forms no exception to this rule. In *Simocephalus* and *Sida* among the Cladocera the ventral chain consists of two longitudinal cords united by transverse commissures, and giving off separate nerves to mandibles, first maxillae, and the swimming appendages. In the adults of these genera the central nervous system is not more than half the length of the body, though in the young state the proportion is much greater.* In *Leptodora* the ventral ganglia are fused into a

common mass. The motor nerves to the first antennae arise from, or can be traced to (*Apus*) the brain, those of the second antennae arise from the oesophageal commissures, or the suboesophageal ganglion (Fig. 250).

The Branchiopods possess a pair of large eyes which are frequently compound and sometimes fused together in the middle line. In the Anostraca they are stalked and movable (Sars). In other forms, though superficial in the larva, the eye is covered in by a fold of skin which, growing from behind, forms an open (*Apus* and *Estheridae*) or closed (Cladocera) chamber over it (Grobben). In addition a small median simple eye (nauplius eye) may persist. The first antennae bear *olfactory* papillae in the Cladocera.

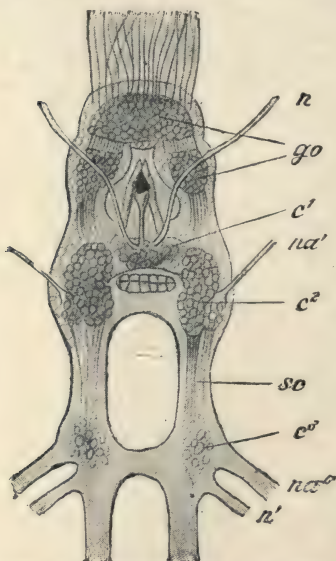


FIG. 250.—Ventral aspect of the brain of *Daphnia similis* (from Korschelt and Heider, after Claus). c^1 and c^2 divisions of the supraoesophageal ganglion; c^3 suboesophageal ganglion; go optic ganglion; n nerve to the sensory organ of the neck; na^1 nerve to 1st antenna; n^1 and na^1 nerves to 2nd antenna; so oesophageal commissure.

A group of sensory hairs in front of the median eye constitutes the *frontal organ*; and groups of ganglion cells in connexion with the skin are found on the forehead (*Branchipus*) or at the sides of the neck (Cladocera).

Many members of the group have the power of attaching themselves to surrounding objects by means of peculiar patches of glandular cells situated on the dorsal surface (*cervical gland*), near the fold separating the carapace from the head shield.

* Cf. Cunningham, *Simocephalus*, *Jen. Zeits.*, Bd. 37.

The *heart* is elongated and segmented in the Phyllopoda (Fig. 247), saccular in the Cladocera (Fig. 251). Coiled excretory organs known as *shell glands* (Figs. 248 and 251, *s d*) from the fact that their coils often lie between the lamellae of the shell, are always present, and in the cases where the duct has been traced (*Limnadia* and *Apus*), open to the exterior on the posterior maxillae. The antennary glands, though present in the larvae of Phyllopods (Claus), are not functional in adult Branchiopoda.

Respiration is performed by the entire surface of the body the area of which is much increased by the reduplication of the skin forming the carapace, by the foliaceous swimming feet, as also by their more specialized lobes, the proximal epipodites.

Reproduction.—The Branchiopoda are of separate sexes.* The males are distinguished from the females by the structure of the first pair of antennae which are larger and more richly provided with olfactory hairs, or by the prehensile character of the second antennae (Anostraca), or (Cladocera, Conchostraca) by the character of their anterior swimming feet which are armed with prehensile hooks. In general the males are less frequently met with than the females, and, in some cases only at certain seasons of the year.

In the Cladocera, and in the genera *Apus*, *Artemia* and *Limnadia* among the Phyllopoda, many generations consisting entirely of females and reproducing parthenogenetically succeed one another. In the Cladocera this is generally the case during the early summer. In the late summer and autumn mixed broods consisting of males as well as females, and broods of males are produced. From the fertilized "resting" or "winter" eggs which are now produced, the parthenogenetic broods of the following year arise.

Weismann concludes that in the Daphnidae the succession of broods forming the life cycle is definite for each species, and adapted to its mode of life. Thus in species inhabiting large bodies of water, such as lakes, many parthenogenetic female broods succeed one another during the summer, and it is only on the onset of cold weather in autumn that males are produced. Species which multiply in puddles on the other hand may present only a single parthenogenetic generation.

Issakowitsch has recently published † a preliminary account of some

* The statement which has recently been made, that *Apus* is hermaphrodite, does not rest on satisfactory evidence. Hermaphrodite forms sometimes, however, make their appearance in the Cladocera, cf. p. 379.

† Geschlechtsbestimmende Ursachen bei den Daphniden, *Biol. Centralblatt*, Bd. 25, No. 16, 1905.

interesting researches, undertaken with the purpose of finding the answer to the question, "On what does the onset of the sexual period in the life-cycle of the Daphnidae depend?" and has arrived at results differing considerably from those of Weismann. He finds that when the parthenogenetically produced offspring of one parent (*Simocephalus vetulus* O.F.M.) are divided into two batches, and, while kept at a warm temperature, are submitted, the one to conditions of abundant nourishment, the other to a starvation diet, those in the first batch continue to reproduce females by parthenogenesis, while those in the second produce males, or winter eggs. The second result is also produced by cold, even when food is abundant, but Issakowitsch is inclined to attribute it to the falling off in nutrition resulting from the lower rate of metabolism. He concludes that "nourishment and temperature (the latter by its influence on nourishment) are the determining factors for the occurrence or disappearance of the sexual individuals; and that there is no cyclical succession of generations in the Daphnidae."

The conditions under which males are produced, in the above named Phyllopod genera, are more obscure. The presence of males in a colony of the genus *Apus* is of rare occurrence. Thus an examination of the successive generations of *A. cancriformis* inhabiting pools in certain clay pits, carried on for six consecutive years failed to reveal to von Siebold a single male among 8,521 specimens which he examined. Colonies are however occasionally found in which males are present, though always in smaller numbers than the females. In some species of *Artemia* males are also of rare occurrence, while in others they are plentiful. The males of *Limnadia Hermannii* Brongn. are unknown.

The females usually carry the eggs about with them on appendages specially modified for this purpose (*Apus*), or in a brood pouch beneath the shell on the dorsal surface (Daphnidae), or in ventral marsupia (*Branchipus*).

In the Phyllopoda the young leaves the egg as a somewhat modified nauplius larva, with three pairs of appendages (the mandibular palp, which is absent in the adult, being at this stage well developed); and the mature condition is reached by a complicated metamorphosis. In the Cladocera, on the other hand, whose large eggs contain abundant yolk and are protected in the brood pouch of the mother, the young are hatched in the form of the adult, though passing through a nauplius stage within the egg. That remarkable and aberrant form *Leptodora* offers however an exception to this rule in that while the summer eggs develop in this manner, the winter eggs (which are fertilized) hatch out as nauplius larvae (Sars.)

A few Cladocera live in the sea, but the greater number of Branchiopods inhabit bodies of freshwater where there is little or no current. Some of them are found in brine pools.

Sub-Order 1. PHYLLOPODA.*

Branchiopoda, with clearly segmented body, often enclosed in a flat shield-shaped or laterally compressed bivalve shell, with from ten to thirty or more pairs of foliaceous swimming feet bearing saccular epipodites.

The **alimentary canal** is provided with two lateral hepatic appendages which are as a rule branched and racemose and only exceptionally short and simple. The **heart** is a long dorsal vessel with numerous paired lateral slits which may extend along the whole length of the body (Fig. 247). The **genital organs** which are always paired are placed by the side of the alimentary canal and open at the boundary between the thorax and abdomen, a limit which may or may not be marked by other structural features. In the Branchipodidae they are simple, but in *Apus* they are racemose glands in both sexes. In the females the genital openings are small slits; in the males of the Anostraca there are protrusible copulatory organs at the openings.

The males may be distinguished from the females in the Conchostraca by the fact that the anterior or two anterior pairs of legs are armed with hooks, and in the Anostraca by the large size of the posterior antennae, which in *Branchipus* and *Branchinecta* are moreover beset with peculiar appendages. In *Apus* they are distinguished by the absence from the 11th pair of appendages, of the brood pouch, to be referred to directly. The eggs are generally protected during development, being carried about the body of the mother either in a projecting uterine dilatation of the united oviducts, at the base of the abdomen (Branchipodidae), which, unlike the egg-sack, of the Copepoda, is a cellular structure opening by muscular lips; or between the valves of the shell attached to filiform processes

* Schäffer, *Der Krebsartiger Kieferfuss* etc., Regensburg, 1856. A. Kozubowski, Ueber den männlichen *Apus cancriformis*, *Arch. für Naturgesch.*, Bd. 23, 1857. C. Claus, *Zur Kenntniss des Baues und der Entwicklung von Branchipus und Apus* etc., Göttingen, 1873. The same, Untersuchungen über die Organisation und Entwicklung von Branchipus und Artemia, *Arbeiten aus dem zool. Institute, Wien.*, Bd. 6, 1886. A. S. Packard, *A monograph of North American Phyllopod Crustacea*, Washington, 1883.

of the 9th and 10th pairs of legs (*Estheria*), or in box-like brood pouches borne on the 11th pair of thoracic appendages, at the base of which the oviducts terminate. These are formed by the apposition of the flabellum and a rounded concave plate projecting from the distal portion of the limb (*Apus*).

In the eggs of *Branchipus* the segmentation is complete at any rate in the early stages. The nauplius larva is characterized by several peculiarities. Its body is, in *Branchipus* and *Estheria*, distinctly divided into a cephalic and post-cephalic region; the upper lip is extraordinarily large; the first pair of antennae is usually rudimentary and sometimes even absent, while the second pair is exceptionally large (Balfour).

Almost all the Phyllopoda belong to inland waters, and principally inhabit shallow fresh-water pools. When the latter dry up the eggs lying in the dry mud may retain their power of development for years.

Tribe I. ANOSTRACA.

Body cylindrical, without carapace; eyes pedunculated; second antennae prehensile in the male; 11-19 pairs of thoracic legs bearing two or three exites; small paired copulatory appendages in the male; the female carries the eggs in a ventral egg sac in which the oviducts terminate. Widely distributed in fresh and salt water lakes.

Fam. 1. **Branchipodidae**. Abdomen distinctly segmented in both sexes, with paired caudal appendages; prehensile antennae of male distinctly jointed; 11 pairs of thoracic legs, usually with 2 exites (3 in *Chirocephalus*). *Artemia* Leach, in salt water lakes*; *Artemiopsis* G.O. Sars; *Branchinecta* Verrill; *Branchipus* Schäff (Fig. 247); *Chirocephalus* Prev. occurs in Britain; *Branchipodopsis* G.O.S.; *Branchiopsilus* G.O.S.

Fam. 2. **Thamnocephalidae**. Abdomen terminates in a broad swimming plate. *Thamnocephalus* Packard, N. America.

Fam. 3. **Polyartemiidae**. Abdomen of female imperfectly segmented; prehensile antennae of male not jointed; 19 pairs of thoracic appendages, with three exites. *Polyartemia* Fischer, with vestigial mandibular palp in *P. forcipata*. Tundras of N. Europe and Asia and Alaska.

Tribe 2. NOTOSTRACA.

Shell shield-shaped fused in front with the head shield; lateral eyes

* It has been stated that it is possible, by diminishing the salinity of the water inhabited by a colony of *Artemia salina* to induce changes in their characters so that they assume those of the genus *Branchipus*. The evidence in support of this statement has however been shown to be quite insufficient. Cf. Bateson, *Materials for the Study of Variation*, p. 96; Grochowski M. Ueber eine neue im Süßwasser lebende Species von *Artemia*, *Verh. Zool. Bot. Ges., Wien*, 1895, p. 95. See also Samter and Heymons, Variationen bei *Artemia salina*, *Abh. Akad. Berlin*, 1902, *Anh.* 2.

dorsal, not stalked; caudal fork consisting of two long jointed appendages; both pairs of antennae simple and rudimentary; two pairs of maxillae are present. There are 40–63 pairs of legs diminishing from before backwards, and furnished with two exites; the terminal appendages of the most anterior pair are long and antenna-like; and the 11th are modified to form round brood-pouches in the female (cf. p. 376).

Single fam. **Apodidae**. *Apus* Schöff. without median caudal lamella. *Lepidurus* Leach, with a median caudal lamella, and larger carapace, but the 2 genera closely allied. Many spp. known from fresh waters in many parts of the world.

Tribe 3. CONCHOSTRACA.

A bivalve shell is present in which the whole of the rest of the body may be completely enclosed. Lateral eyes not stalked, approximated. First antennae simple, small or rudimentary; second large and biramous. 10–28 pairs of post-cephalic limbs are present, of which the first, or the first and second pairs, are provided with prehensile hooks in the male. The eggs are carried between the hinder part of the body and the shell, attached to dorsally directed processes of some of the limbs.

Fam. 1. **Limnadiidae**. Shell compressed, marked with lines of growth; body elongated, with 16–28 pairs of thoracic legs. *Limnadia* Brong.; *Eulimnadia* Packard; *Estheria* Rüpp.; *Leptestheria* G.O.S. *Cyclestheria* G.O.S.

Fam. 2. **Limnetidae**. Shell tumid, without lines of growth; head very large; body short; not more than 12 pairs of legs. *Limnetis* Lovén.

Sub-Order 2. CLADOCERA. Water-fleas.*

Small laterally compressed Branchiopoda, whose body, with the exception of the head, which projects freely, is usually enclosed in a bivalve shell. The second antennae are large and are used in swimming, and there are four to six pairs of swimming feet. The epipodites may be absent.

The Cladocera are small simply organized Branchiopoda, whose resemblance to the larvae of the shelled Phyllopods, particularly to that of *Estheria* with its six pairs of legs, probably gives the best indication of the origin of the group. Unlike

* Besides the work of F. Leydig already quoted compare H. E. Strauss-Dürkheim, "Mémoire sur les Daphnia de la classe des Crustacés," *Mem. du Mus. d'hist. nat.*, Tom. V and VI, 1819 and 1820. Leydig, *Naturgeschichte der Daphniden*, Tübingen, 1860. P. E. Müller, *Bidrag til Cladocerernes Fortplantings historie*, Kjöbenhavn, 1868. G. O. Sars, "Om endimorph Udvikling samt Generationsvexel hos Leptodora," *Vidensk. Selsk. Forh.*, Christiania, 1873, p. 1. A Weismann, *Beiträge zur Kenntniss der Daphniden*, I—VII, *Z. f. w. Z.*, Tom. 27, 28, 30 suppl. and 33, 1876–1880. C. Claus, *Zur Kenntniss der Organisation, etc., der Daphniden*, *ibid.*, 27, 1876. C. Claus, *Zur Kenntniss des Baues und der Organisation der Polyphemiden*, Wien, 1877. C. Grobben, *Die Embryonalentwicklung von Moina rectirostris*, *Arbeiten aus dem zool. Institut*, Wien, II Band, 1879. W. A. Cunningham, *Studien an einer Daphnide*, *Jena. Zeits.*, T. 37, p. 447, 1903.

the anterior antennae, which are usually short, the posterior are modified to form biramous swimming appendages beset with numerous long setae. The four to six pairs of legs are not always foliaceous swimming feet, but in some cases have the form of cylindrical ambulatory or prehensile appendages. The abdomen, which is ventrally flexed, develops on its dorsal side several

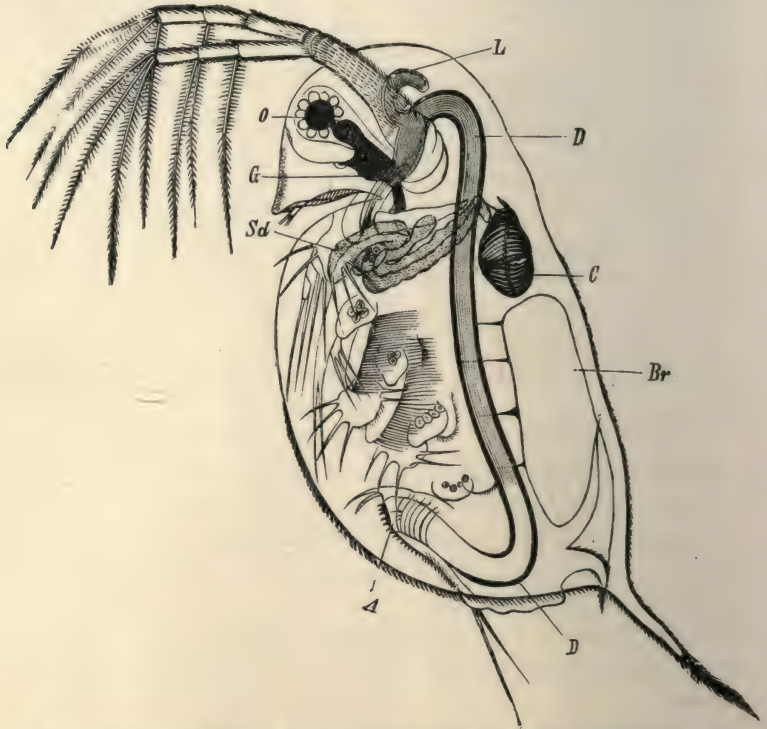


FIG. 251.—*Daphnia*. *A* anus; *Br* brood-pouch beneath the dorsal reduplication of the shell; *C* Heart—the slit-like opening of one side is visible; *D* alimentary canal; *G* cerebral ganglion; *L* paired hepatic diverticulum; *O* paired eye; *Sd* shell gland. (After Claus.)

prominences, which serve to close the brood pouch. It usually consists of three free segments, together with the terminal anal portion, which is beset with rows of hooks. The anal portion begins with two dorsal tactile setae and ends with two hooks or styles, representing the caudal fork of other Entomostraca (Fig. 251).

The internal organization is simple in correspondence with the small size of the body. The compound eyes (*O*) fuse together in

the middle line to form a large, continually trembling, frontal eye, largely developed in the Polyphemidae. Beneath this the unpaired simple eye, reduced in *Daphnia* to a streak of pigment in connection with the brain, usually remains. A special sensory apparatus, whose function is not quite clear, appears in the region of the neck, in the form of an aggregation of ganglion cells.

The **heart** has the form of an oval sac, with a pair of transverse lateral venous ostia and an anterior arterial opening. Its pulsations are rhythmic, and succeed one another quickly. In spite of the want of arteries and veins, the blood, which contains amoeboid cells, circulates along definite channels in the body. The looped and coiled **shell gland** (*Sd*) is always present. The cervical gland, which functions as an organ of attachment, is less widely distributed. The **sexual glands** lie in the thorax as paired tubes by the side of the alimentary canal. In the ovaries groups of four cells are separated; in the formation of the summer-eggs one cell of each group, usually the third from the front end, becomes an ovum, while the rest are employed as nutritive cells for the nourishment of the ovum, which increases in size and absorbs fat globules. In the formation of the winter-eggs every other group of four cells, or a larger number, likewise breaks up and subserves the nourishment of the cells destined to become the eggs (Weismann). The ovary is directly continuous with the oviduct, which opens dorsally beneath the shell into the brood-pouch. The testes, like the ovaries, lie at the sides of the intestine and are continuous with the vasa-deferentia, which open to the exterior ventrally by a common opening behind the last pair of appendages or at the extreme end of the body, the openings being sometimes situated on small slightly protrusible prominences.

The smaller males usually appear in the autumn; they may, however, also be present at any other time of the year, and, as recent investigations have proved in a tolerably satisfactory manner, always when the conditions of life and nourishment are unfavourable (vide p. 373). Before the appearance of the males, hermaphrodite forms * are sometimes produced with an organization which is partly male and partly female.

At the season when males are not present, normally in the

* Compare especially W. Kurz, Ueber androgyne Missbildung bei Cladoceren, *Sitzungsber der Akad. der Wissensch.* Wien, 1874.

spring and summer, the females produce the so-called summer eggs, which contain a large quantity of oil globules and are

surrounded by a delicate vitelline membrane. They develop rapidly within the brood-pouch between the shell and the dorsal surface of the mother, and after the space of only a few days develop into a fresh generation of young Cladocera, which escape from the brood-pouch. The embryonic development takes place accordingly under extremely favourable conditions, which depend upon the rich supply of food yolk in the large eggs, and sometimes upon additional food material secreted within the brood-pouch.

At the season when the males appear, the females, independently of copulation, begin to produce so-called winter eggs, which are incapable of developing without fertilization. The

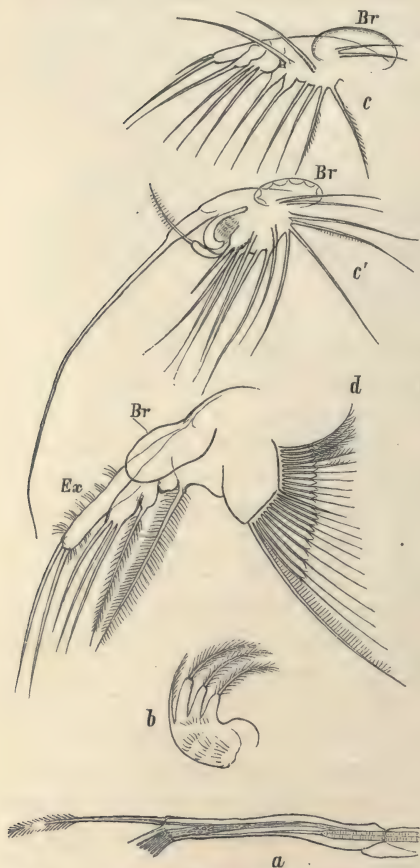


FIG. 252.—Appendages of *Daphnia* (after Claus).
a, anterior antenna of male; b, maxilla; c, first leg of female, c', of male; d, a leg of the 2nd pair; Br bract; Ex exopodite.

number of these winter eggs is always relatively small. They are distinguished from the summer eggs by their larger size and the greater quantity of food yolk, and their formation in the ovary is accompanied by much more extensive processes of absorption. Before the eggs pass into the brood-pouch, the walls of the latter, which as above stated are formed by the dorsal and posterior portions of the bivalve shell, become modified over a

saddle-shaped area, the cuticle acquiring a firm consistency and brown colour. At the next moult after the eggs have entered the brood-pouch, they are contained in the shed cuticle, the bivalved thickened region or *ephippium* remaining as a protective case for the eggs after the rest of the cuticle has disintegrated.

The Cladocera live for the most part in fresh water, and certain species inhabit deep inland lakes. Others live in brackish water and the sea. They swim quickly, and usually with a jumping movement. Some of them attach themselves to fixed objects by means of the dorsal "cervical gland" (p. 372). When the body is thus fixed, the swimming feet are able by their rhythmic movements to set up currents in which small food particles are swept towards the animal.

Fam. 1. **Sididae**. Heart elongated. Gut straight. 6 pairs of similar lamellate legs, with well developed epipodites. *Latona* Straus, *Daphnella* Baird, *Penilia* Dana, *Limnosida* Sars, *Sida* Straus, with large cervical adhering apparatus. *Holopedium* Zadd., 2nd antennae unbranched.

Fam. 2 and 3. **Daphnidae** and **Lynceidae**. Heart shortly oval, gut with a direct course in *Daphnidae*, coiled in *Lynceidae*; 5 or 6 pairs of limbs, the lamellar character and the branchial appendages becoming more developed from before backwards. (*Daphnidae*) *Ilyocryptus* Sars, *Acantholeberis* Lilljeb.; *Bosmina* Baird, anterior antennae long, a sixth (rudimentary) pair of legs is present; *Drepanothrix* Sars, *Macrothrix* Baird, *Lathonura* Lilljeb.; *Moina* Baird, anterior antennae large and prehensile in the ♂ of *M. paradoxa*; *Scapholeberis* Schödl., *Ceriodaphnia* Dana, *Simocephalus* Schödl.; *Daphnia* Müll., the head shield not separated from the shell by a groove (Fig. 251). (*Lynceidae*) *Eurycercus* Baird, with 6 pairs of legs, *Camptocercus* Baird, *Acroperus* Baird, *Alonopsis* Sars, *Alona* Baird, *Phrixura* Müll., *Pleuroxus* Baird, *Chydorus* Leach, *Monopsilus* Sars.

Fam. 4. **Polyphemidae**. The shell does not enclose the body and legs as in the other families of the Cladocera, but is small and usually only contains the brood chamber. Head bluntly rounded, with very large compound eyes. Legs slender, distinctly jointed, branchial appendages rudimentary. Marine and freshwater. *Podon* Lilljeb. and *Evadne* Lovén with 4 pairs of short legs crowded together. Abdomen rudimentary, covered by the shell. *Polyphemus* Müll. and *Bythotrephes* Lilljeb. The second antennae, four pairs of legs, and the abdomen are much elongated. The legs with rudimentary branchial appendages. *Leptodora* Lilljeb. The head and posterior part of the body elongated and the latter distinctly segmented. The 6 pairs of cylindrical unbranched legs on the contrary are crowded together, the anterior pair being long. 1st antennae long and comb-like (sensory) in the ♂, 2nd antenna large, with stout basal joints. The summer eggs develop directly in the brood-pouch into the form of the adult, but the (fertilized) winter eggs hatch out as nauplius larvae. Fr. w. lakes of N. Europe.

Order 3. OSTRACODA.*

Small, usually laterally compressed Entomostraca, with a bivalve shell and usually with seven pairs of appendages, which serve as antennae, jaws, creeping and swimming legs. There is a large mandibular palp, and a short abdomen ending in a simple plate or a caudal fork.

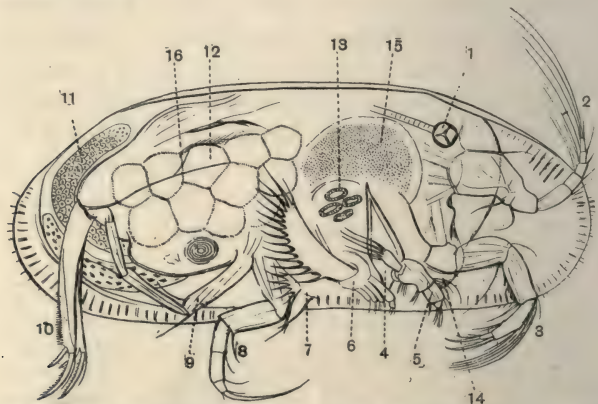


FIG. 253.—*Stenocypris malcolmsonii* (Brady). (= *Cypris cylindrica* Baird). The right half of the shell has been removed. 1 median eye; 2 anterior antenna; 3 posterior antenna; 4 mandible; 5 mandibular palp; 6 first maxilla; 7 second maxilla; 8 and 9 thoracic appendages; 10 caudal fork; 11 ovary; 12 advanced ova; 13 bundles of fibres of adductor muscle; 14 upper lip; 15 stomach; the caecal diverticulum of the left side is seen in the fold of the shell below 11; 16 the leader points a little below the intestine. (After G. O. Sars.)

The body of these small Crustacea is unsegmented and is completely enclosed in a bivalve shell, which gives the animal a resemblance to a mussel. The surface of the shell may be smooth, or variously sculptured, or beset with setae. In the

* Besides Straus-Dürkheim, Fischer, Lilljeborg, Baird and others compare W. Zenker, Monog. d. Ostracoden, *Arch. f. Naturgesch.*, XX, 1854. G. O. Sars, Oversigt af Norges marine Ostracoder, *Vid. Selsk. Forh. Christiania*, 1865. C. Claus, *Beit. z. Kenntniss d. Ostracoden. Entwicklungsgesch. v. Cypris*, Marburg, 1868. Id. *Die Halocypriden des atlantischen Oceans und Mittelmeeres*, Wien, 1891. Id. *Beitr. z. Kenntniss d. Süswasserostacoden*, I and II, *Arb. Zool. Inst. Wien*, 1892 and 1895. G. S. Brady, A monograph of the recent British Ostracoda, *Trans. Linn. Soc.*, London, XXVI., 1868. Id. *Ostracoda, Challenger Rep.*, 1, 1880. A. Kaufmann, *Beitr. z. Kenntniss d. Cytheriden*, *Receuil Zool. Suisse*, iii, 1886. O. Nordqvist, *Beitr. z. Kenntniss d. inneren männlichen Geschlechtsorgane d. Cypriden*, *Act. Soc. Sc. Fenn.*, xv, Helsingfors, 1885. G. S. Brady and A. M. Norman, Monog. of the Marine and Fresh-water Ostracoda of the N. Atlantic and of N.W. Europe. 1. Podocopa. *Trans. R. Dublin Soc.* (2) vol. 4 (1889), p. 61. G. W. Müller, *Die Ostracoden d. Golfes v. Neapel*. (Naples Monograph No. 21), Berlin, 1894. Id. *Deutschlands Süswasserostacoden*, *Zoologica*, 1900.

Halocypridae it is richly supplied with glands. The two valves of the shell are joined together by an elastic ligament along the middle third of the back, and the action of this ligament is opposed by a two-headed adductor muscle, which passes from one valve of the shell to the other and causes impressions discernible from without (Fig. 253, 13). The tendon common to the two heads of the muscle lies nearly in the middle of the body. The edges of the valves are free at both ends and along the ventral side. In the free-swimming marine Cypridinidae (Fig. 254) and Halocypridae there is a deep indentation in the edges of the valves, to allow the antennae to pass out. When the valves of the shell are open, several pediform appendages can be protruded on the ventral side, which enable the animal to move in the water either by crawling or by swimming. The abdomen can also be protruded; it either ends in a caudal fork (*Cypris* and *Cythere*), or has the form of a plate armed with spines and hooks on its posterior margin (*Cypridina*).

Appendages.—Anterior antennae, uniramous.

Posterior antennae, biramous.

Mandibles, with a usually biramous palp.

First maxillae, usually jaws (in Polycopidae short biramous legs).

Second maxillae, jaws, maxillipeds, or legs.

Sixth pair of appendages, jaws, or legs, or 0.

Seventh pair of appendages, legs, or specially modified, or 0.

Eighth pair of appendages, represented by the brush-shaped organs in the males of Podocopa, by the penis in Cypridinidae (Müller).

The two pairs of *antennae* are placed on the anterior region of the body (Figs. 253, 2 and 3, and 254, A', A''), and are used as creeping or swimming legs. In the Cypridinidae and Halocypridae the *anterior* pair is provided with large olfactory hairs. The *second* pair of antennae are generally the most important organs of locomotion. In the exclusively marine Cypridinidae and Halocypridae they have the form of biramous swimming feet, and consist of a broad triangular basal plate, a many-jointed exopodite beset with long swimming setae, and a reduced endopodite, which, however, is stronger in the male and furnished with hooks of a considerable size. The Polycopidae have the two rami approximately equal in size, while in the other families the endopodite is the principal ramus, the exopodite being reduced

or absent altogether (G. W. Müller). In these (Fig. 253, 3) the appendages resemble legs, and end with strong hooked bristles, by help of which the animal can attach itself to surrounding objects.

In the region of the mouth, beneath and to the side of a tolerably large upper lip, there are two *mandibles* usually with a broad and strongly toothed biting edge. In one division of the Ostracods—the Myodocopa—the mandibles have the form of legs rather than jaws. In the Cypridinidae even the masticatory process on the basal joint may disappear, or be represented by a small setose lobe (Fig. 254), while the palp has the form of a strong leg. In the other division, the Podocopa, the palp though still pediform has more moderate proportions, and may be biramous (Fig. 253, 5). In exceptional cases (*Paradoxostoma*), the mandibles are styliform and are enclosed in a suctorial proboscis formed from the upper and under lips.

The appendages which follow the mandibles are very variously modified in the different families of Ostracods in relation to the function of mastication, or to locomotion or to both combined. The *fourth* pair, or *first maxillae*, are jaws in all except the small family Polycopidae, where they have the form of short legs carrying a distinct outer ramus. In the Podocopa they carry a large comb-like setose plate which by its movement promotes the process of respiration, though it does not itself act as a gill (Fig. 253, 6). The *second maxillae* (*fifth pair*) are jaw-like in the Cypridinidae and carry an enormous respiratory plate (Fig. 254). In the Halocypridae and Cypridae they have an intermediate character between jaws and locomotory limbs, the basal joint being stout and carrying a respiratory fan (small in *Cypris*), and the endopodite forming a jointed appendage directed backwards from it and provided with stiff claw-like setae. In the Cytheridae the whole appendage is more slender and leg-like. In the Polycopidae, where this is the last pair of appendages, they are short and leg-like, and carry a respiratory fan.

The appendages of the *sixth* pair are again jaw-like in the Cypridinidae, in the Cypridae and Cytheridae they are leg-like, while in the Halocypridae they have an intermediate character. The *seventh* pair are leg-like in the Cypridae and Cytheridae. In the former family they occupy a peculiar position (Fig. 253, 9),

being turned upwards and backwards over the hind part of the body and carry a brush of setae at the end. In the Cypridinidae

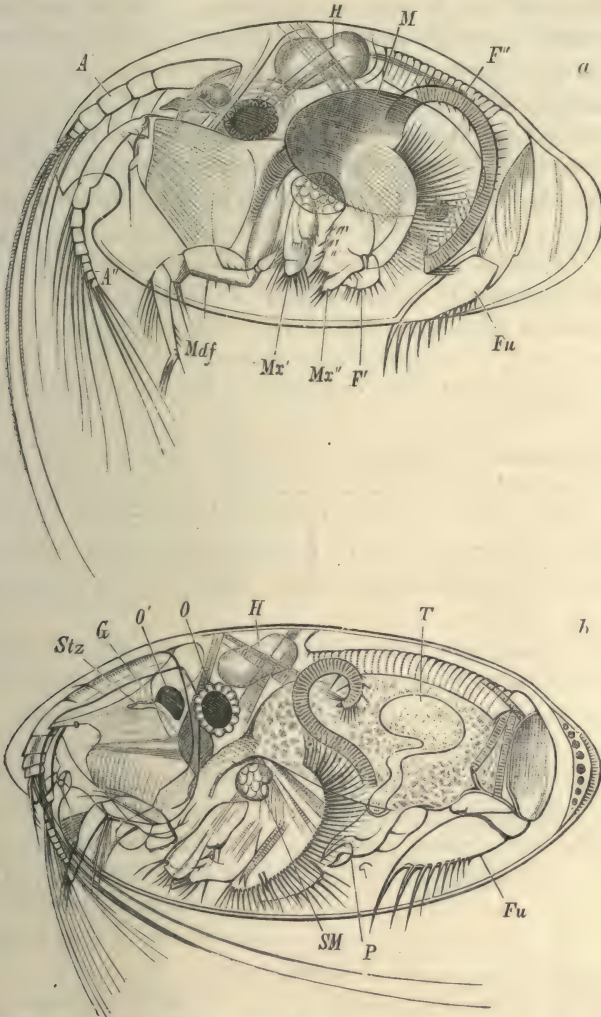


FIG. 254.—*Cypridina mediterranea*. *a* Female; *b* male. *A'*, *A''* first and second antennae; *F'*, *F''* first and second thoracic legs; *Fu* caudal fork; *G* brain; *H* heart; *M* stomach; *Mdf* mandibular palp; *Mx'* first maxilla; *Mx''* second maxilla; *O* eye; *O'* unpaired eye; *P* copulatory organ; *SM* adductor muscle; *Stz* frontal organ; *T* testis. (After Claus.)

(Fig. 254, *F''*) this pair of appendages is long, cylindrical and many-jointed; they also carry a terminal brush of setae, and as

in the Cypridae are directed upwards over the hind part of the body and beneath the shell. In both families they probably have the function of keeping the hinder part of the interior of the shell clean (Putzfuss). In the Halocypridae these appendages are represented by long slender flagella.

A pair of short and stalked "brush-shaped organs" with sensory functions, which are present in the males of the Podocopa, are regarded by Müller as the representatives of an *eighth* pair of appendages. In the Cypridae and Cytherellidae they lie behind the seventh, but in other Podocopa they are situated in front of them. In the Cypridinidae they probably enter into the formation of the penis (Fig. 254b, P).

The **nervous system** consists of a bilobed cerebral ganglion and a ventral chain with closely approximated pairs of ganglia. A suboesophageal mass supplies nerves to the mandibles and first maxillae.

Sense organs. In addition to the olfactory hairs and "brush-shaped organs" already mentioned **eyes** are generally present. Except in the Halocypridae the unpaired or *nauplius eye* is present, consisting of a ventral median and two lateral elements which may be united in the middle line or, as in some Copepods, quite distinct.

In the Cypridinidae (Fig. 254, O) there is in addition a pair of compound lateral eyes consisting of a number (4-50 or more)

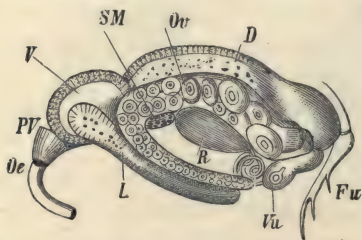


FIG. 255.—Alimentary canal and generative organs of a female *Cypris* (from Claus, after W. Zenker). *D* intestine. The opening of the anus, which is not seen here, is dorsal to the caudal fork. *Fu* caudal fork; *L* liver; *Oe* oesophagus; *Ov* ovary; *PV* crop; *R* receptaculum; *SM* adductor muscle; *V* stomach; *Vu* vulva.

of separate elements. The Halocypridae and Polycopidae are without eyes. In the Cyprinidae a peculiar median, rod-shaped organ, the *frontal process* (*Stz*) projects forward, in the neighbourhood of the nauplius eye.

Alimentary canal. The mouth, which is frequently (*Cypris*) armed with

toothed lateral bands, leads through a narrow oesophagus into a dilated crop-like portion of the alimentary canal (Fig. 255), which in *Bairdia* is developed into a regular masticatory mill. This is followed by a broad and long stomach pro-

vided with two long lateral hepatic tubes (*L*), which may project between the lamellae of the shell. The anus opens near the base of the abdomen either dorsal or ventral to the caudal fork.

A saccular **heart** is present in most *Myodocopa* on the dorsal surface, where the shell is connected with the body. It is absent in most if not all *Podocopa*. The function of **respiration** is performed by the inner lamella of the shell, as well as by the whole surface of the body, over which an uninterrupted current of water is maintained by the swinging movements of the fan-shaped setose plates. There are no true branchiae on the appendages, but in some *Cypridinidae* there is a double row of leaf-like branchial structures on the back, near the last pair of limbs.

Two sets of glandular structures which appear to correspond with the *excretory organs* of other *Entomostraca* are described by Claus. An extensive gland, sending a process between the lamellae of the shell, has been traced into the base of the posterior antennae, though the opening was not detected. Smaller glands opening on the basal joint of the second maxillae correspond with the shell glands of other forms, though in the *Ostracods* they do not extend into the shell. The so-called *Spinn-drüsen* of the *Cytheridae* which open on the elongated exopodite (vide infra, *Cytheridae*) of the second antenna belong, apparently, to the category of cutaneous glands.

Generative organs. The sexes are always separate and are distinguished by well-marked differences in structure. The males possess appliances on different appendages—in *Cypridina* on the second antennae, in *Cypris* on the maxilliped—for holding the females; or a pair of legs (the first thoracic) may be modified for this purpose (*Halocypridae*). In addition a large copulatory organ, often possessing a complicated structure, is always present. It is, however, not homologous in the several families, as will appear below. In the *Cypridinidae* the testes are simple rounded bodies and the vasa deferentia run directly to a median opening common to them both just in front of the anus. A pair of appendages situated on either side of the opening and probably representing the brush-shaped organs of some of the *Podocopa* is, in this family, modified as copulatory organs. In the *Cypridae* there are four elongated or rounded lobes of the testis on either side, and the vasa deferentia are connected by a canal passing from one to the other, which may be of great length and thrown

into complex folds. The part of the vas deferens nearer the opening has a chitinous wall, and at its commencement a peculiar ejaculatory apparatus is situated which in the fresh-water forms is a large and complex organ. This was formerly known as the "mucous gland." At its termination the vas deferens traverses the corresponding half of the (paired) penis, the end of it being protrusible. In Halocypridae and Polycopeidae the penis is traversed by the vas deferens but is single, and situated to one side of the middle line. The spermatozoa are very long in some species, in *Pontocypris monstrosa* they are, according to Müller, 5-7 mm. in length, or 8-10 times as long as the body of the animal. The female of *Cypris* possesses two ovarian tubes which project between the lamellae of the shell (cf. Fig. 253), two receptacula seminis, and the same number of genital openings at the base of the abdomen. As in the Copepoda the receptacula seminis are often provided with two ducts; one by which the spermatozoa are introduced, and the other communicating with the oviduct.

In addition to the sexual characters noted above differences in the shape of the shell, and the richer endowment of the male with sensory organs may be noted.

Development. The greater number of Ostracoda lay eggs which they either attach to water-plants (*Cypris*) or, as in *Cypridina*, carry about with them between the shell valves until the young are hatched. *Parthenogenesis* has been recognized as occurring among the Cypridae by Weismann and by G. W. Müller. According to Woltereck * it is, in some species, of the kind found in the Daphnidae, in which a number of parthenogenetic generations succeed one another during the summer, to be followed in the autumn by a sexual generation. In *Cypris reptans* however the sexual generation has never been seen. Cultures of this species have been under observation for eighteen years in the Freiburg laboratory, yet a male has never been recognized.

The free development of *Cypris* consists of a complicated metamorphosis. The larvae, when hatched, possess, like nauplius larvae, only three pairs of appendages, but they are strongly compressed laterally, and are already enclosed in a thin

* R. Woltereck Zur Bildung und Entwicklung d. Ostrakoden Eier, *Zeit. f. wiss. Zool.*, Bd. 64 (1898), p. 596.

bivalve shell (Fig. 256). In the marine Ostracoda the development is simplified so that the metamorphosis is entirely absent.

The Ostracoda feed partly on animal and partly on vegetable matter.

Numerous fossil Ostracods are known from almost all formations, but only the remains of their shells are preserved. They abounded in the Silurian seas and attained there a much larger size (90 mm.) than any known existing genera. The deep-sea expeditions of recent years have however brought to our knowledge the large free-swimming Cypridinid *Gigantocypris* (q.v.), which attains a length of 23 mm.

Ostracods resemble one or other of the groups of Phyllopods in the following features:—the bivalve shells closed by an adductor muscle; the saccular heart, situated in front of the point of reflection of the shell; the presence of compound eyes in the Cypridinidae; the large setose plates attached to some of the postoral appendages; the large upper lip of the nauplius larva and the retarded development of the second maxillae.

On the other hand the highly specialized condition of the mouth parts of the adult Phyllopoda—the absence of the mandibular palp and the reduced maxillae—finds no parallel in the Ostracods, for in these the mandibular palp is more leg-like in character than in any other group of Crustacea, and the same is true, though in a less degree, of both maxillae. In association with these apparently primitive features in the Ostracods, we may bear in mind the leg-like character of the second antennae, and in the Myodocopa, of the mandibles, though these may very possibly be adaptive features. The presence of a bivalve shell in the nauplius larva is another feature in which the two groups stand contrasted.

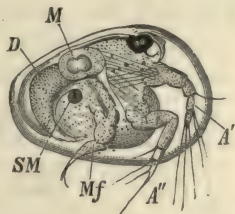


FIG. 256.—Very young larva of *Cypris* (after Claus). Nauplius stage, with three pairs of appendages. A', A'' first and second antennae; D intestine; M stomach; Mf mandible; SM shell muscle.

Sub-order 1. MYODOCOPA.*

The shell is notched in front to give play to the antennae. The basal joint of the second antenna is usually wide, and the

* The name Myodocopa (μυώδης muscular, κώπη an oar) is given by Sars in allusion to the expanded muscular base of the second antenna, which

many jointed exopodite is the longer of the two rami. The mandibular palp is long and pediform. A respiratory plate is absent from the first maxilla, but present on the second. The halves of the caudal fork are plates bearing spines along their margins, gradually increasing in size towards the terminal extremities of the plates.

Fam. 1. **Cypridinidae**. Shell hard, the notch for the antennae situated at or below the middle of the dorso-ventral extent of the shell. First antenna strongly flexed at the articulation between the basal joint and the next. Mandible without a regular masticatory process, this being represented by a small lobed setose plate connected with the basal joint. The large 4-jointed pediform palp bears a small exopodite. The three following appendages are all short and more or less jaw-like and aggregated about the mouth region. The 7th is a many-jointed worm-like structure, the end beset with bristles. Generative orifice single and median. In the male the copulatory organ consists of a pair of structures probably representing a pair of appendages, which arise on either side of the orifice. A heart, two large compound eyes, together with a median eye and rod-like "frontal organ," are present. *Cypridina* M. Edw. (Fig. 254), some spp. phosphorescent. *Pyrocypis* Müll., *Crossophorus* Brady, *Gigantocypis* Müll., *G. Agassizii*, obtained by U.S. ss. "Albatross" and since by the "Valdivia," is probably a free-swimming inhabitant of deep water. It is nearly globular in shape, orange in colour, and provided with a pair of mother-of-pearl like plates over the eyes. It attains a length of 23 mm. *Philomedes* Lilljeb., *Pseudophilomedes* Müll., *Cylindroleberis* Brady, *Sarsiella* Norm.

Fam. 2. **Halocypridae**. Shell calcified; the notch for the antennae situated above the middle of the dorso-ventral extent. Numerous unicellular glands, opening on the surface, are present along the margins of the shell. Mandible with well-developed masticatory process. 1st maxillae jaw-like; 5th pair of appendages (mx. 2) with a backwardly directed endopodite, and a respiratory fan on the protopodite; the sixth are leg-like; while the seventh are slender, dorsally directed structures bearing a few bristles. The vasa deferentia unite in a duct traversing the penis which lies on the right of the middle line. A heart and "frontal organ" are present, but eyes are absent. Pelagic. *Thaumatocypis* Müll., *Conchoecia* Dana, *Halocypis* Dana, *Euconchoecia* Müll., *Archiconchoecia* Müll.

Fam. 3. **Polycopidae**. The halves of the shell are round or oval, and the antennary notch shallow or absent. Second antennae with a comparatively narrow basal joint, and approximately equal rami. Mandible with a weak masticatory process. The fourth pair of appendages (mx. 1) are not masticatory and bear a well-developed exopodite; the fifth (which is also the last pair) are short and carry a large respiratory fan. The penis is markedly unsymmetrical. Heart, eyes and frontal organ are absent. Minute Ostracods living at the bottom of the sea. *Polycope* Sars, *Polyopsis* Müll.

is here a swimming organ and, as in some other Entomostraca, one of the principal organs of locomotion. In the Podocopa these appendages are leg-like.

Sub-order 2. **PODOCOPA.***

The shell is not notched in front, and, in accordance with the creeping habit, is flattened along the ventral border. The second antenna articulates with a prominence at the side of the upper lip. The endopodite forms the strong leg-like termination of this appendage, while the exopodite is short, and generally much reduced. The mandible has a short palp which may be biramous (Fig. 253).

Fam. 4. **Cypridae**. Shell generally not sculptured. The endopodite of the second antenna is strongly flexed on the basal joint and terminates in strong claw-like setae; the exopodite is reduced to a small scale. The fourth pair of appendages (1st maxillae) is jaw-like, having masticatory processes from the basal joint, a short palp and a large respiratory fan (epipodite). The next pair has a masticatory process and a respiratory fan on the basal joint, a short exopodite directed forwards and a longer claw-like endopodite directed backwards. The latter is modified as a prehensile organ in the male. The sixth pair is long and pediform: the seventh, is also pediform but slender and directed dorsally. The halves of the caudal fork slender and rod-like, bearing setae at their ends, or reduced. There is no heart. The testes and ovaries are partly contained between the lamellae of the shells. In the males a peculiar ejaculatory apparatus formerly known as the "mucous gland," invests the vas deferens near its termination. The greater number of species live in fresh water. *Notodromas* Lilljeb., with the three parts of the median eye widely separated, *Cypris* Müll., *Stenocypris* Sars (Fig. 253), *Pontocypris* Sars, *Pontocypris* Müll., *Ilyodromus* Sars, *Argilloecia* Sars, *Paracypris* Sars, *Candona* Baird, *Macrocypris* Brady, *Aglaia* Brady, *Goniocypris* Brady, *Metacypris* Brady, *Nesidea* Costa.

Fam. 5. **Bairdiidae**. A small group of marine *Podocopa* with characters intermediate between those of the *Cypridae* and *Cytheridae*. The shell is frequently much arched dorsally and the two halves are unsymmetrical. The crop forms a well-developed masticatory mill. *Bairdia* McCoy, *Bythocypris* Brady, *Anchistrocheles* Brady and Norman.

Fam. 6. **Cytheridae**. Shell strongly calcified. Second antenna like that of the *Cypridae*, but the exopodite is an elongated and slender organ, bent at the tip, and perforated by the duct of the large unicellular "spinning-gland," the secretion of which is, according to Müller, spread as a web of fibres over surrounding objects. The fourth pair of appendages (mx. 1) has a masticatory function, but the three following are exclusively locomotory. Divisions of the caudal fork small and weak. There is no heart and neither the testes nor ovaries extend between the lamellae of the shell. All the species are marine. *Cythere* O. F. Müll., *Eucythere* Brady, *Cythereis* Sars, *Cytherideis* Jones, *Cytheretta* G. W. Müll., *Microcytherura* G. W. Müll., *Cyprideis* Jones, *Krithe* Brady, Crosskey and Robertson, *Cytheropteron* Sars, *Loxoconcha* Sars, *Pseudoloxoconcha* G. W. Müll., *Cytheroma* G. W. Müll., *Xestoleberis* Sars, *Microxestoleberis* G. W. Müll., *Paracytheridea* G. W. Müll., *Polycheles* Brady, *Cytherura* Sars,

* See footnote on p. 389.

Eucytherura G. W. Müll., *Sclerochilus* Sars; *Cytherois* G. W. Müll., the members of this and the two following genera have suctorial mouth parts and live on the juices of water-plants. *Paradoxostoma* Fisch., *Paracytherois* G. W. Müll.; *Microcythere* G. W. Müll., *Bythocythere* Sars, *Pseudocythere* Sars, *Paracythere* G. W. Müll., *Jonesia* Brady, *Normania* Brady, *Limnocythere* Brady.

Fam. 7. **Cytherellidae.** This family, consisting of the single marine genus *Cytherella* Bosq. apparently represents a primitive form of the *Podocopa*. The regularly arranged thickened bands in the hinder part of the body give rise to a suggestion of segmentation, but this appears not to correspond with the segmentation indicated by the limbs. The outer ramus of the 2nd antenna is larger than in other *Podocopa*, and the brush-shaped organs of the male, which probably represent an eighth pair of appendages, are situated behind the last pair of limbs. The divisions of the caudal fork are lamellar and fringed with stout bristles.

Fam. 8. **Darwinulidae.** This consists of a single fresh-water species *Darwinula stevensoni* Brady and Robertson. The anatomy is not completely known, but the species appears to be allied to the Cypridae.

Order 4. COPEPODA.*

Entomostraca with elongated, usually well segmented body, without shell-forming reduplications of the skin, and with biramous swimming feet.† The abdomen is without appendages, and the eggs are usually carried by the female in single or paired sacks attached to the anterior abdominal segment.

The order consists of a very large number of species of small active free-swimming crustacea, and of a variety of forms which have to a large extent lost their power of free locomotion and live as external parasites on other animals. While many of the latter present no great departures from the type of structure met with in the free-living groups, in others the Copepod and

* O. Fr. Müller, *Entomostraca seu Insecta testacea, quae in aquis Daniae et Norvegiae reperit, descripsit*, Lipsiae, 1785. Jurine, *Histoire des Monocles*, Genève, 1820. W. Lilljeborg, *De crustaceis ex ordinibus tribus: Cladocera, Ostracoda et Copepoda, in Scania occurrentibus*, Lund, 1853. C. Claus, *Die freilebenden Copepoden*, Leipzig, 1863. C. Grobben, *Die Entwicklungsgeschichte von Cetoichilus septentrionalis*, *Arch. des Zool. Instituts*, Wien., Tom 3, 1881. C. Claus, Ueber die Maxillarfüsse der Copepoden etc., *ibid.* 11, Heft. 1 (1895). M. H. Hartog, The Morphology of Cyclops, etc., *Trans. Linn. Soc.* Vol. V. pt. I. p. 1 (1888). W. Giesbrecht, Die pelagischen Copepoden etc., *Fauna and Flora des Golfes von Neapel*, 1892. *Idem.*, *Asterocheridae*, *ibid.*, Bd. 25, 1899. Giard, Sur le parasitisme des Monstrillidae, *Comptes Rendus*, T. 123 (1896), p. 836. Malaquin, Le parasitisme évolutif des Monstrillidae, *Arch. Zool. exp.* (3), T. 9, p. 81. Hansen, *Choniostomatidae*, Copenhagen, 1897.

† The name Copepoda has reference to the oar-like character of the divisions of the swimming feet in the free-living forms.

indeed the Arthropod character is entirely masked in the females, the bodies presenting an ungainly and monstrous appearance with little indication of limbs or of segments. The males of these species are however of more normal structure and the affinities are always clearly indicated in the characters of the young.

The free-swimming forms superficially resemble the macrurous Decapod Crustacea in the general contour of their body (Fig. 257). This consists of a more or less oval anterior portion, including the cephalothorax and a number (3-5) of movable thoracic segments, bearing swimming feet; and of a narrower posterior portion, the abdomen, which is without appendages. It ends in a caudal fork, consisting of two lateral processes, beset with setae.

The first abdominal segment carries the generative orifices. The hind part of the body is generally divided off by a constriction which in some forms (*Gymnoplea*) lies behind the last (5th) thoracic segment, but in others (*Cyclopidae*, *Harpactidae*) in front of it. The region behind the constriction is called by some authors the *urosome*. In the latter case the last thoracic segment is included in the *urosome*. In the former the *urosome* is identical with the abdomen.

The cephalothorax and the anterior free thoracic segments are produced laterally, in *Cyclops*, into low pleural folds (Hartog). In female *Notodelphyidae* (q.v.) a dorsal brood sack is formed in the thoracic region.

In the free-swimming forms the number of segments of the body, as indicated by paired appendages or by the jointing of

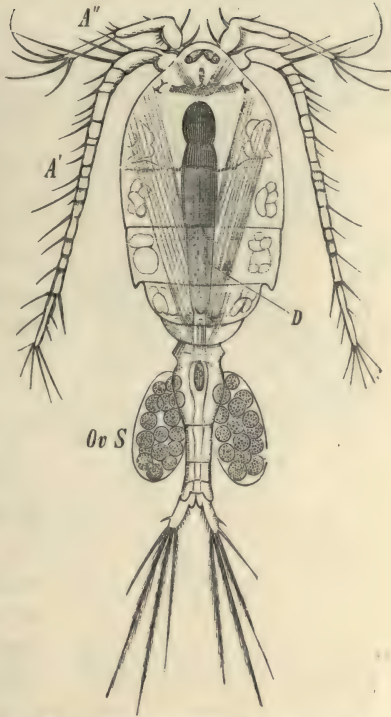


FIG. 257.—Female of *Cyclops coronatus* seen from the dorsal surface (after Claus). *A'*, *A''* the anterior and posterior antennae; *D* alimentary canal; *Ov S* egg sacks.

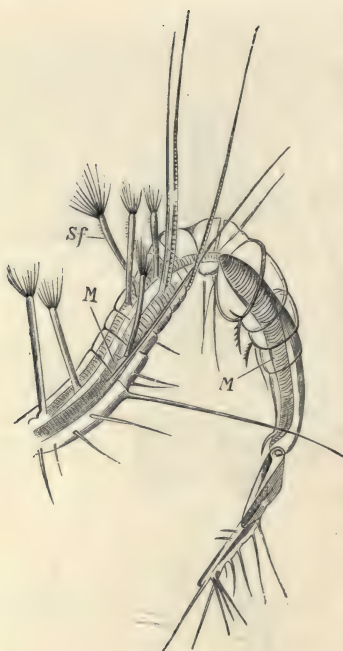


FIG. 258.—An anterior antenna of the male *Cyclops serrulatus* (after Claus). *Sf* olfactory organs, *M* muscles.

racic segments are fused with the head. Behind the second come four other thoracic segments, bearing swimming feet, but the two last may be fused together. In the females of many Calanidae the sixth thoracic feet are absent, and in the Cyclopidae and Harpactidae they are rudimentary, the segment to which they belong being included, as we have seen, in the urosome.

From the early investigation of Claus into the anatomy and development of members of the Cyclopidae it was concluded that the two pairs of appendages following the first maxillae are not two pairs but the inner and outer divisions of a single pair. It was pointed out that though in the majority of Copepods they are inserted separately on the body, in *Cyclops* their bases are actually united (Fig. 259). This

the cuticular skeleton, or both, is fairly constant, though departures from the usual number are frequently met with, especially in the abdomen, and the number may differ in the sexes of a single species.

The cephalothorax terminates in front in a ventrally directed pointed or forked rostrum. It bears two pairs of antennae, mandibles, two pairs of maxillae and a pair of maxillipeds. Posteriorly it may be distinct (some Calanidae) from the second thoracic segment (Fig. 260), but generally two anterior tho-



FIG. 259.—Mouth parts of *Cyclops*. *Kf'* second maxilla; *Kf''* maxilliped (first thoracic appendage); *M* mandible; *Mx* first maxilla (after Claus).

view was resisted by Hansen and by Giesbrecht, and was finally abandoned by Claus himself.*

It has been shown that in the larval history of members of the Calanidae (Fig. 263) these two pairs of appendages are not only separate from their origin, but that a segmental furrow of the body lies between them—which is, in fact, the division between head and thorax—and that there are distinct ganglia corresponding to them. It is clear therefore that the approximation of these appendages found in *Cyclops* and its allies is a departure from the more generalized condition found in the Calanidae, a conclusion which is borne out by a general view of their relationship. We are now, therefore, able to name the anterior pair (the inner in *Cyclops*) second maxilla, while the posterior (outer in *Cyclops*) or "hand" of Jurine, must be regarded as the first thoracic appendage, modified to carry food to the mouth, and hence to be named the maxilliped.

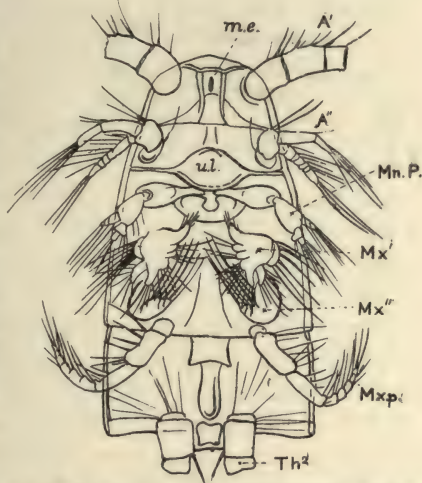


FIG. 260.—Ventral aspect of the anterior part of the body of *Calanus finmarchicus* L. A' first antenna; A'' second antenna; me median eye; Mn.p mandibular palp; Mx' first maxilla; Mx'' second maxilla; Mx.p maxilliped; Th² bases of the first pair of swimming feet, united by "coupler"; u.l. upper lip. (After Sars.)

The abdomen is generally five-jointed in males and four-jointed in females. The first segment carries the openings of the generative ducts, and the anus is situated on the last segment, in the angle between the two divisions of the caudal fork. The abdomen, especially in the parasitic forms, very frequently undergoes a considerable reduction.

Appendages.—Anterior antennae, uniramous.

Posterior antennae, uni- or biramous.

Mandibles, generally with a well-developed and sometimes biramous palp.

First maxillae.

Second maxillae.

Maxillipeds or 1st thoracic appendages, uniramous.

Second thoracic appendages (biramous swimming legs).

Third " " " "

Fourth " " " "

Fifth " " " "

Sixth " " " "

The anterior antennae arising on either side of the base of the

* Arb. aus. d. zool. Inst. Wien, xi, 1.

rostrum are usually many-jointed (25 in *Gymnoplea*) and, by their powerful strokes, propel the animal by leaps through the water. They are beset with olfactory structures, and in the male one or both may be modified as a prehensile organ for catching and holding the female (Fig. 258). They are never biramous. The *posterior antennae*, which are always the shorter, are in some families biramous (Fig. 260). In the parasitic Lernaevidae and their allies, they serve as organs of attachment to the host (Fig. 266).

The *mandibles*, in the free-living forms have a toothed blade (basal joint) projecting inwards on either side into the mouth, and a simple or biramous (Fig. 260) palp, which however in *Cyclops* is reduced to little more than a group of bristles (Fig. 259). An upper lip projects in front of the mouth and a bilobed lower lip may be present behind it. In the parasitic forms the lips are produced and applied together to form a conical suctorial apparatus within which the palps, styliform and piercing mandibles are contained (Lernaepodidae and Caligidae). In *Philichthys* and its allies only the upper lip is produced. The *first maxillae* lie behind and external to the mandibles, and are in the Calanidae lobed structures resembling a Phyllopod appendage (cf. Fig. 260). In *Cyclops* they are more jaw-like (Fig. 259), and in the parasitic forms are much reduced, and situated on the outer surface of the sucking tube. The *second maxillae* and the *maxillipeds* are uniramous. In the free forms the maxillipeds are generally the longer and the terminal portion can be folded on the basal joints (the "hand" of Jurine). They are especially modified as prehensile organs in the males of the Corycaevidae in which group the anterior antennae are not adapted in this manner. In the females of the parasitic Lernaepodidae they are generally long and arm-like, ending in a horny disc, common to the pair, by which the animal is attached to the host (Fig. 264, c).

The *swimming feet* consist of a two-jointed basal portion, and two three-jointed, setigerous, flattened rami (Fig. 261). The coxopodites of these appendages are often intimately connected by a median plate, or "coupler," regarded by Hartog as a prolongation downward of the sternite of the segment (Fig. 260). In the parasitic groups the swimming feet are much reduced, and in some entirely absent. In several free forms while the anterior swimming feet are well developed

the fifth pair is much reduced (*Cyclops*) or absent. In many Calanidae though absent in the female, it is in the male modified, unsymmetrically, as a pair of copulatory organs.

It will be noticed that when five pairs of swimming feet are present, the number of the appendages corresponds with that found in the Cirripedes.

The **nervous System** consists in the Calanidae of a supra-oesophageal ganglion, supplying the eyes and anterior antennae, a circumoesophageal ring giving off nerves to the second antennae, and a chain of seven or fewer median ganglia behind the oesophagus, of which the two anterior supply the mandibles, maxillae and maxillipeds. In the Corycaeidae however and in the parasitic forms the ganglia are concentrated into a ring round the oesophagus from which a single or double cord, in which ganglion cells are present, is continued backwards.

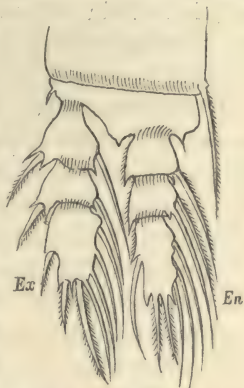


FIG. 261.—A swimming foot of *Cyclops*. *En* endopodite; *Ex* exopodite.

Sense organs. A median frontal eye (*nauplius* or *Cyclops eye*) is present (Figs. 257 and 260), though lost in the later stages of parasitic forms. It is divided into three parts, paired dorsal and median ventral, and the former are provided with cuticular lenses. In the pelagic Pontellidae the median eye is highly developed and provided with deep and cuticular lenses. The lateral divisions of it are also largely developed in the Corycaeidae. In the Branchiura alone among the Copepoda compound lateral eyes are present (Fig. 267) in addition to the median eye.

Delicate **olfactory** hairs and rods are present on the anterior antennae, principally in the male (Fig. 258).

Phosphorescent organs. Some pelagic Copepods (some Pontellidae and *Oncaea*) emit bright sparkles of greenish or bluish light, produced by the contact of the secretion of skin-glands with the water. These are present also in the larvae, and the arrangement of the glands and the colour of the light is characteristic of the species.*

* Giesbrecht, Mitth. üb. Copepoden 8. Ueb. d. Leuchten d. pelagischen Copepoden, *Naples, Mitth.*, Bd. 11, p. 648 (1895).

The **alimentary canal** is divided into a short narrow oesophagus, a wide stomach often with two anterior diverticula, which are sometimes ramified, and an intestine opening in the angle of the caudal fork. Hepatic cells lie in the walls of the stomach, and posterior to these is a tract the cells of which contain urinary secretions. The stomodaeal cuticle only extends over the anterior one-third of the stomach (Hartog).

Excretory organs. The *antennal glands* which open at the base of the 2nd antenna of the nauplius are only present in the larva of these as of most other Entomostraca. Glands which also have an excretory function have been found in some genera at the sides of the anterior part of the cephalothorax, and in the Eucopépoda they have been found to open, as usual, on the 2nd maxillae (Richard).

A saccular heart is present in the Calanidae and Pontellidae, but generally a heart is absent, the movement of the blood being effected by the regular oscillations of the intestine. There are no special respiratory organs (unless the lateral processes of the hind part of the body in the parasitic *Pennella* are to be so regarded).

Generative organs. The Copepoda are of separate sexes. In both the generative organs lie in the cephalothorax and the free thoracic segments and open (except in the Choniostomatidae, q.v.) right and left in the basal segment of the abdomen. The males as a rule are smaller and more active than the females. Sexual differences in the form and structure of different parts of the body, such as the modifications in the males of the anterior antennae, maxillipeds or sixth thoracic appendages have been already noted. In the free-swimming genus *Copilia* (Corycaeidae) the body is cylindrical in the female, flattened in the male.

But sexual dimorphism of a different nature may also be present to a marked degree. Some species among the pelagic families are beset with setae of such elaborate development and brilliancy of colouring that it appears impossible to regard them as other than ornamental (vide Plates I-IV in Giesbrecht's *Pelagischen Copepoden des Golfes von Neapel*, *Fauna and Flora*, vol. xix.). What makes the occurrence of such elaborate ornamentation in this group

more remarkable is, besides the minute size of the animals, the fact that the structure of the eyes is so simple that it appears inconceivable that their owners should be in any degree aware of the ornamentation presented by their fellows. In some species both sexes are similarly ornamented (e.g. *Augaptilus fligerus*, Claus), in others the male alone is brilliantly coloured (*Sapphirina*), but in several of the most marked instances it is the female which is conspicuously decorated (*Calocalanus*, *Copilia*) while the males are comparatively plain. Some details of the ornamentation are given below under the separate families.

In contrast with this kind of dimorphism is that found among the parasitic Copepods. While in some families the sexual differences are slight, in *Lernaea* (as the result of fertilization) and in the Chondracanthidae and Lernaeopodidae (independently of that event, Fig. 265) the female grows to a large size, acquiring a monstrous, distorted appearance in which its Copepod characters are completely masked, while the minute males, dwarfs in comparison, retain more of their original characters and frequently live, attached by their hooked appendages to the body of the female.

The *testes* and *vasa deferentia* may be single or paired. The spermatozoa are elongated bodies twisted about their long axis. They are contained in spermatophores, which are formed in the lower part of the vas deferens. During copulation, which is only an external approximation of the two sexes, the male fastens one or more spermatophores on the genital segment of the female. The *ovary*, like the testis, may be single or paired, but the oviduct is always paired. A cement gland is generally present at its termination which also performs the office of a spermatheca where this organ is not separately developed. A separate duct, to the orifice of which the spermatophore is attached by the male, leads into the spermatheca (or cement gland). Through this the spermatozoa are injected by the expansion (owing to the inhibition of water) of a fluid contained in the spermatophore. The eggs are fertilized in the lower end of the oviduct, and a mass of them becomes enveloped in the secretion of the cement glands, which hardens in the water. The egg sacks so produced are single or paired, and may be oval or fili-form (Figs. 257 and 266, *d*). In some cases however the eggs are laid singly, and in the Notodelphyidae they develop in the

dilated oviducts (uteri) contained in a dorsal expansion of the posterior thoracic region. In *Cyclops* one fertilization suffices for many broods (Hartog). Firm-shelled eggs are produced by *Diaptomus* towards the end of the reproductive period, and pass through a latent stage before hatching (Wolf).

Development takes place by means of a complicated metamorphosis, which, in many parasitic forms, is a retrograde one. The larvae have, when hatched, the nauplius form, with an

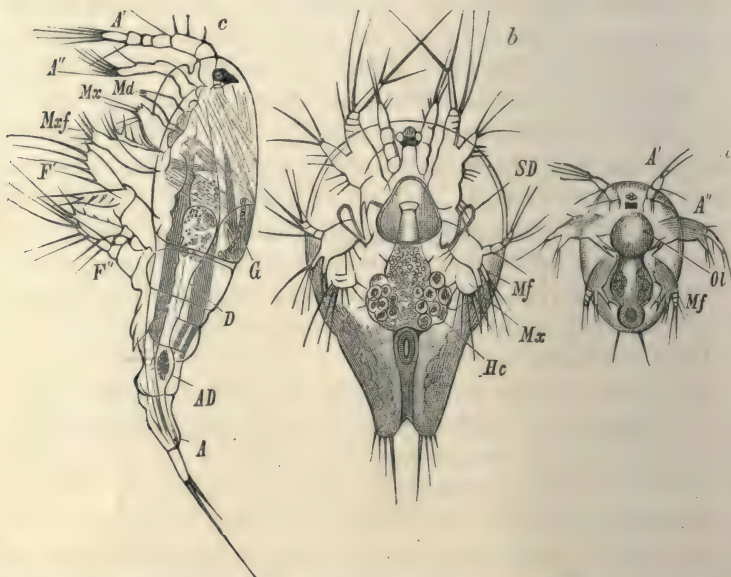


FIG. 262.—Metamorphosis of *Cyclops*. *a* Nauplius larva of *Cyclops serrulatus*, after hatching; *b* older stage, more highly magnified; *c* very young *Cyclops* form. *A* anus; *A'*, *A''* first and second antennae; *AD* rectum; *D* intestine; *F'*, *F''* first and second swimming feet (second and third thoracic appendages); *G* rudimentary gonads; *Hc* urinary concretions; *Md*, *Mf* mandible; *Mx* first maxilla; *Mxf* maxilliped (partially hiding the second maxilla); *Ol* upper lip; *SD* antennal gland. (From Claus.)

unpaired frontal eye and three pairs of appendages. Hooked setae on the second and third pairs of appendages serve to conduct the food into the mouth, which is covered by a large upper lip (Figs. 242 and 262, *a*). The posterior region of the body is destitute of appendages, and terminates with two setae at the sides of the anus; it includes the thorax and abdomen, which are as yet undifferentiated. The antennary glands act as excretory organs.

The alterations undergone by the larvae in the course of

their further growth are connected with a number of successive moults, and consist principally in an elongation of the body and the appearance of fresh appendages. In the next larval stage (*metanauplius*, Fig. 262, b), a fourth pair of appendages, the future first maxillae, makes its appearance behind the three original pairs, which develop into the antennae and mandibles. In a later stage four fresh pairs of appendages are formed (Fig. 263). Of these the first and second correspond to the second maxillae and maxillipeds, while the third and fourth represent the first rudiments of the anterior swimming feet. The functional limbs still resemble those of a nauplius, and it is after another moult that the transformation into the first Cyclops-like form occurs. It then resembles the adult animal in the structure of the antennae and mouth parts, although the number of the appendages and of the body rings is still incomplete (Fig. 262, c). The last two pairs of appendages already have the form of short biramous swimming feet, and the rudiments of the third and fourth pairs of swimming feet have made their appearance as projections beset with setae.* The body consists in this stage of the oval cephalothorax; of the second, third and fourth thoracic segments; and of an elongated terminal portion, which gives rise to the last thoracic segment and to all the abdominal segments by progressive segmentation. It already terminates in the caudal fork.

Many forms of parasitic Copepoda, for example *Lernanthropus* and *Chondracanthus* (Fig. 265), do not get beyond this stage of body segmentation, and obtain neither the swimming feet of the

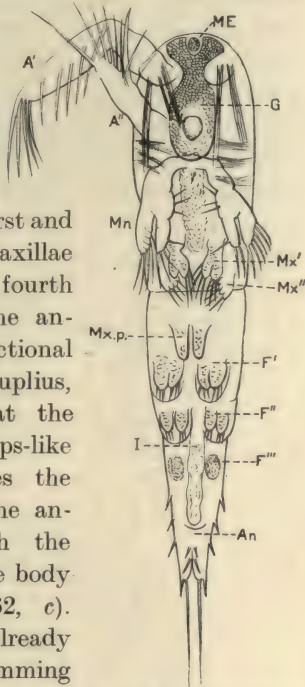


FIG. 263.—Metanauplius of *Calanella*. A', A'' first and second antennae; An anus; F', F'', F''' the three anterior swimming feet (thoracic appendages 2-4); G brain; I intestine; ME median eye; Mn mandibles; Mx', Mx'' first and second maxillae; Mx.p maxilliped (first thoracic appendage). After Claus.

* Hartog finds that the setae are formed inverted, and that they become everted when a larval skin is shed.

third and fourth pairs, nor a fifth thoracic segment distinct from the stump-like abdomen; others, for example *Achtheres*, by the loss of the two anterior pairs of swimming feet, sink back to a still lower stage (Fig. 264).

All the non-parasitic and many of the parasitic Copepoda pass in successive moults through a larger or smaller number of developmental stages, in which the still undeveloped segments and appendages make their appearance, and the appendages already present undergo further segmentation. Many parasitic Copepoda, however, pass over the later series of nauplius forms,

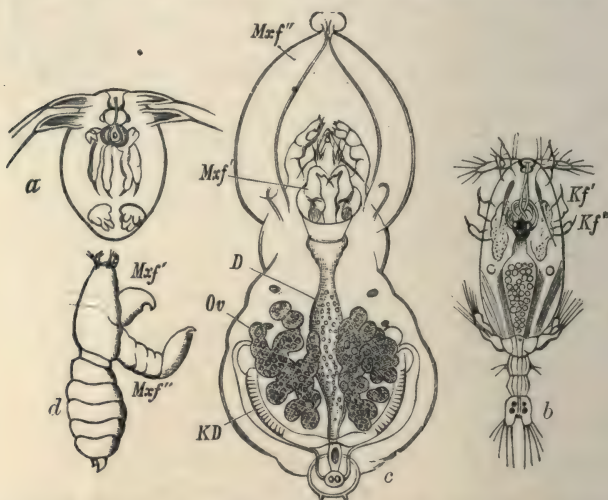


FIG. 264.—*Achtheres percarum*.—*a* Nauplius form. *b* Larva in the youngest Cyclops stage; *Kf'* second maxillae and *Kf''* maxillipeds; *c* Female seen from the ventral side; *Ov*, ovaries; *KD* cement glands; *d* The smaller male seen from the side; *Mxf'*, *Mxf''* second maxillae and maxillipeds. From Claus.

and the larva, as soon as hatched, undergoes a moult, and appears at once in the youngest Cyclops form, with antennae adapted for adhering and mouth parts for piercing (Fig. 264). From this stage they undergo a retrogressive metamorphosis, in which they become attached to a host, lose more or less completely the segmentation of the body which grows irregular in shape, cast off their swimming feet, and even lose the eye, which was originally present (Lernaeopoda). The males, however, in such cases often remain small and dwarfed, and adhere firmly (frequently more than one) to the body of the female in the region of the genital opening (Fig. 265).

In *Lernaea* (Fig. 266) such pigmy males were for a long time vainly sought for upon the peculiarly shaped body of the large female (Fig. 266, c, d) which carries egg tubes. At last it was discovered that the small Cyclops-like males (Fig. 266, a) lead an independent life and swim about freely by means of their four pairs of swimming feet, that the females (Fig. 266, b), in the copulatory stage resemble the males, and that it is only after copulation that they (the females) become parasitic and undergo the considerable increase in size and modification of form which characterizes the female with egg-tubes.

Monstrilla and its allies pass through a very remarkable life-history. The adult forms are pelagic animals, destitute of alimentary canal, mouth parts and second antennae. The nauplius attaches itself to the bodies of sedentary Polychaetes, and casting off its appendages penetrates into the vascular system of the host, in which all further stages in the development supervene, though without casting a skin (Malaquin*).

Nourishment is taken in by means of the second antennae and

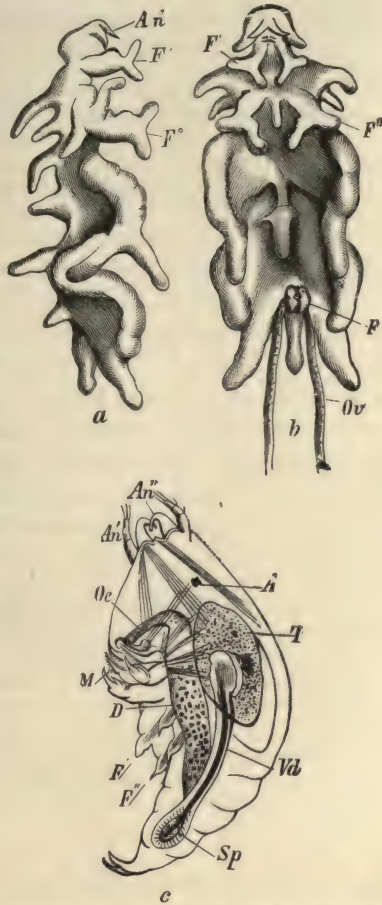


FIG. 265.—The two sexual animals of *Chondracanthus gibbosus* magnified about six diameters. a Female seen from the side; b from the ventral surface with adhering males; c male strongly magnified. A eye; An' anterior antennae; An'' posterior antennae (for attachment); D intestine; F', F'' the two pairs of thoracic feet. M mouth parts; Oe oesophagus; Ov egg-tubes; Sp spermatophore; T testis; Vd vas deferens. From Claus.

* Malaquin, Le parasitisme évolutif des Monstrillides, *Arch. Zool. exp.* 3, T. 9, p. 81.

sometimes by the mandibles as well, which reappear and grow out into long tentacular appendages, comparable in their function with the root-like appendages of the Cirripede Rhizocephala. Having attained the adult stage the animals throw off these appendages, and leave the body of the host to assume their brief pelagic existence, which comes to an end after the maturation and discharge of the sexual products.

Sub-order 1. EUCOPEPODA.

Copepoda with masticatory or suctorial mouth parts, and swimming feet the branches of which are two- or three-jointed.

The seventeen families into which the Eucopepoda have been divided are arranged (following Gerstaecker) in six series. The first consists of free-swimming forms; the fourth, fifth and sixth of parasitic forms. In the second and third series while some members are free-living, others are adapted to a commensal or semiparasitic mode of life. A much larger number of families is recognized by more recent writers, but no complete classification of the sub-order is at present available.

The first two families, the Pontellidae and Calanidae, are included by Giesbrecht in his group *Gymnoplea*, which is characterized by the following features. They are free and powerfully swimming pelagic Copepods with long and many-jointed (24–25) anterior antennae, and biramous posterior antennae. 5th and 6th thoracic segments closely united and separate from the urosome, and in the male the appendage of the 6th modified, often unsymmetrically, as copulatory organs; urosome, 5-jointed in male; male organs unsymmetrical; heart usually present; the eggs are laid separately or carried by the female in a single egg-sack until they are hatched.

First series (Fams. 1–4).

Fam. 1. **Calanidae.** (*Amphaskandria* of Giesbrecht). The anterior antennae of the male are nearly or quite symmetrical, and more abundantly beset with sensory organs than in the female. In the female the 5th pair of swimming feet may be reduced or entirely absent, and the 4th and 5th segments are generally fused.

Calanus Leach, *C. finmarchicus* Gunner (1765), abundant in N. Atlantic (Fig. 260). *Eucalanus* Dana, *Rhincalanus* Dana, *Mecynocera* Thomp., *Paracalanus* Boeck, *Acrocalanus* Giesb., *Calocalanus* Giesb., *C. pavo* Dana; in the female (iv. 15)* the anterior antennae bear long bristles, of which three

* These numbers refer to the plates and figures in Giesbrecht's Monograph on Pelagic Copepods, *Fauna and Flora of the Gulf of Naples*, vol. 19.

at the base are feathery and have a yellow metallic lustre while the terminal one is scarlet. The two divisions of the caudal fork also bear four fan-like feathered appendages almost as long as the body and having a metallic orange colour. The male (I. 13)* is much less strikingly ornamented. The anterior antennae bear very numerous sensory vesicles, and are scarlet at the ends, and the posterior antennae, maxillipeds and the caudal fork bear long narrowly feathered scarlet bristles. In the female of *C. plumulosus* Claus (III. 5)* the anterior antennae and caudal fork bear feathered bristles somewhat similar to those of *C. pavo*, but one of those on the left side of the caudal fork is produced to a length nearly six times that of the body (5.8 mm.) and beset with orange coloured and clubbed setae, forming a delicate flexible appendage of extraordinary beauty. *Clausocalanus* Giesb., *Ctenocalanus* Giesb., *Pseudocalanus* Boeck, *Drepanopus* Brady, *Möbianus* Giesb., *Spinocalanus* Giesb., *Aetidius* Brady, *Gažtanus* Giesb., *Chiridius* Giesb., *Undeuchaeta* Giesb., *Euchirella* Giesb., *Euchaeta* Philippi, *Scolecithrix* Brady, *Xanthocalanus* Giesb., *Phaëna* Claus.

Fam. 2. **Pontellidae** (*Heterarthrandria* of Giesbrecht). One of the anterior antennae of the male, generally the right, modified as a prehensile organ. The 5th pair of swimming feet of the female may be reduced but is never absent. The eyes are often large, sometimes with dorsal and ventral cuticular lenses. The last thoracic and anterior abdominal segments of the male are often unsymmetrical. *Centropages* Kroyer, *Isias* Boeck, *Temora* Baird, *Pleuromma* Claus, *Leuckartia* Claus, *Isochaeta* Giesb., *Disseta* Giesb., *Heterochaeta* Claus, *Hemicalanus* Claus, *Augaptilus* Giesb., *Phyllopus* Brady, *Candace* Dana, *Calanopia* Dana, *Labidocera* Lubbock. *Pontella* Dana, with one pair of eyes provided with cuticular lenses, on the dorsal surface of the head, and additional lenses on the anterior and posterior surfaces of the rostrum. The median ventral element of the eye is also present forming a projection on the ventral surface behind the rostrum. *Anomalocera* Templeton, with each of the lateral elements of the eye double. *Monops* Lubbock, *Pontellina* Dana, *Acartia* Dana, *Corynura* Brady.

Fam. 3. **Harpacticidae**. Free-swimming. Body linear, cylindrical, completely segmented. Last thoracic segment included in the urosome. Both anterior antennae of the male modified as prehensile organs. Posterior antennae usually biramous and with bent setae. Mandibular palp and first maxilla biramous and short. Maxillipeds ending in a hook. The anterior pair of swimming feet may be modified as an additional pair of maxillipeds, the 5th pair leaflike and alike in both sexes. Heart absent. Eye median, simple. Openings of oviducts near the ventral middle line, and egg sack generally median. *Anymone* Claus, *Euterpe* Claus, *Tachidius* Lilljeb., *Longipedia* Claus, *Canthocamptus* Westw. *Dactylopus* Claus, *Thalestris* Claus, *Laophonte* Phil., *Lilljeborgia* Claus, *Jurinia* Claus, *Harpacticus* O. F. Müll., *H. chelifer*, North Sea. *Tisbe* Lilljeb., *Westwoodia* Claus, *Setella* Dana, pelagic. *Clytemnestra* Dana, *Ectinosoma* Boeck, *Sunaristes* Hesse, *Amenophia* Boeck, *Stenhelia* Boeck, *Ameira* Boeck, *Nitocra* Boeck, *Mesochra* Boeck, *Miracia* Dana, *Metis* Phil., *Aenippe* Phil., *Clausia* Clap., *Euryte* Phil., *Idomene* Phil.

* These numbers refer to the plates and figures in Giesbrecht's Monograph on Pelagic Copepods, *Fauna and Flora of the Gulf of Naples*, vol. 19.

Fam. 4. **Peltidiidae**. Free-living marine forms, with feeble swimming power. The body is broad and flattened and the margins of the anterior segments are often produced into overlapping lobes. The cuticle is thick. In other respects they resemble the Harpactidae. *Scutellidium* Claus, *Zaus* Goods., *Alteutha* Baird, *Eupelte* Claus, *Peltidium* Phil. *Porcellidium* Claus, body incompletely segmented. *Hersilia* Phil.

Second series (Fams. 5-8).

Fam. 5. **Cyclopidae**. Marine and freshwater forms with active swimming powers. Body pear-shaped completely segmented. Last thoracic segment included in urosome. Anterior antennae of moderate length, both of them symmetrically modified as prehensile organs in the male (Fig. 258). Posterior antennae uniramous, 4-jointed. Mandibular and maxillary palps reduced. 5th pair of swimming feet cylindrical and alike in both sexes. Heart generally absent. Eye median simple. Egg sacks paired. *Cyclops* Müll. (Fig. 257), mandibular palp reduced to a few bristles (Fig. 259, *M*). Abundant in freshwater pools. *Cyclopsina* Claus. *Oithona* Baird, *O. plumifera* Baird, pelagic. The appendages of the female are beset with long feathery scarlet setae not present in the male. *Misophria* Boeck, *Thorellia* Boeck.

Fam. 6. **Notodelphyidae**. *Cyclops*-like Copepods, with diminished powers of movement, commensal in the interior of Tunicates and other marine animals. Body fully segmented. The anterior antennae of moderate length or with the number of joints reduced to 5. The eggs develop in a wide expansion of the united oviducts (uterus) contained in a large dorsal expansion of the fused 5th and 6th thoracic segments. Cement glands absent. The males are often much smaller than the females. *Notodelphys* Allm. differs from the other genera in having the anterior antennae as long as the cephalothorax. *Doropygus* Thor., *Botachus* Thor., *Goniodelphys* Buchh., *Notopterophorus* Costa, with lamellate dorsal processes on the thoracic segments. *Gunentophorus* Costa, *Chonephilus* Sars, and (?) *Gastrodes* Hesse, and *Ophthalmopaches* Hesse.

Fam. 7. **Ascidicolidae**. Resembling the *Notodelphyidae* in mode of life and in structure except that the body is more elongated, and the anterior antennae are shorter—3-jointed. *Ascidicola* Thor., *Botryllophilus* Hesse, *Narcodes* Hesse, *Ischnogrades* Hesse, *Ophioseides* Hesse, *Enterocola* Bened., *Mychophilus* Hesse, *Adranesius* Hesse, *Aplopodus* Hesse, and (?) *Podolabis*, *Cryptopodus*, *Hypnodes* and *Lygephilus* Hesse. *Enterognathus* Giesb., *E. comatulae* an entoparasite on *Comatula*.

Allied to the *Ascidicolidae* are the forms *Thaumaleus* Kroyer, *Monstrilla* Dana and *Haemocera* Malaquin, whose remarkable life-history is described above (p. 403).

Fam. 8. **Buproridae**. Consisting of the single species *Buprorus loveni* Thor., commensal with *Ascidia aspera* Müll. Allied to the last two families but the body of the female unsegmented.

Third series (Fams. 9-11).

Fam. 9. **Corycaeidae**. Active, marine Copepods, mostly free throughout life, though in some species the females become temporarily attached to other animals. Body cylindrical or flattened. Anterior antennae short, usually 6-jointed, alike in both sexes. The posterior antennae and

maxillipeds are symmetrically modified as prehensile organs, the latter especially in the male. Heart absent. The lateral elements of the eye are often large. The openings of the oviducts are dorsal or lateral. Egg sacks paired. *Lubbockia* Claus; *Oncaea* Philippi; *Corycaeus* Dana. *Copilia* Dana, bodies of glass-like transparency; strongly marked sexual dimorphism; female cylindrical, male flattened; *C. vitrea* Haeckel, in the female (II. 1)* the thoracic appendages bear broad plumose setae which, like the stomach, are of a bright orange colour, and the lateral elements of the eyes have large lenses; the male (L. 8)* is colourless and without lateral eyes. *Pachysoma* Claus. *Sapphirina* J. V. Thompson. Lateral elements of the eyes with cuticular lenses present in both sexes, male much broader than female and brilliantly iridescent (L. 7).* *Sapphirinella* Claus.

Fam. 10. **Ergasilidae**. Copepods in which the females though retaining the power of swimming are parasitic on the gills of fishes and the bodies of mollusca, annelids, etc. The males are probably free at any rate during part of their life. Body cylindrical or flattened, segmented. Anterior antennae 5-7-jointed, postr. antennae modified as grappling hooks, maxillipeds prehensile. The mouth parts are not modified into a sucking tube, and the eye is simple and median. Egg sacks paired. *Doridicola* Leyd., parasitic on *Doris*. *Sepicola* Claus, on squids. *Eolidicola* Sars. *Lichomolgus* Thor. in branchial sacks of tunicates. *Terebellicola* Sars, on Terebellidae. *Eucanthus* Claus. *Bomolochus* Nordm., on pleuronectid fishes. *Ergasilus* Nordm. on teleostean fishes. *Thersites* Pagenst.

Fam. 11. **Ascomyzontidae (Asterocheridae)**. Structure and mode of life resembling that of the Ergasilidae, but the lips are modified into a suctorial apparatus containing the styliform mandibles. Anterior antennae 5-20-jointed, geniculated in the ♂, ant", mx" and mxpd prehensile. The eye may be absent. *Nicotoë* Aud., *N. astaci* with a discoidal proboscis; lives on the gills of the lobster. *Asterocheres* Boeck (*Ascomyzon* Thor.) with a long sucking tube, on tunicates, sponges and echinoderms. *Dyspontius* Thor., *Artotrogus* Boeck, and many others.

Fourth series (Fams. 12-14).

Fam. 12. **Caligidae**. Both sexes live as parasites on the skins of fishes, but are able to swim rapidly. They are broad flattened Copepods of comparatively large size and incompletely segmented. There is a shield-like cephalothorax and the free thoracic segments are often produced into lateral lobes. The genital segment is swollen, especially in the female, and the rest of the abdomen reduced. Anterior antennae short, with 2 or 3 free segments; the basal segment fused with the margin of the cephalothorax. Posterior antennae reduced to a grappling hook, not projecting beyond the margin of cephalothorax. Mandibles styliform, enclosed in a sucking tube. First maxillae free, second maxillae and maxillipeds modified as hooks. 4 pairs of usually biramous swimming feet are present, the 5th pair being often rudimentary or absent. Heart provided with paired valves. Eye, when present, simple and median, or with paired elements. Egg sacks paired and elongated. *Hermilius* Hell., *Parapetalus* Stp. Ltk., *Synestius* Stp. Ltk., *Caligodes* Hell., *Caligus* Müll., *Lepeoph-*

* These numbers refer to the plates and figures in Giesbrecht's Monograph on Pelagic Copepods, *Fauna and Flora of the Gulf of Naples*, vol. 19.

theirus Nordm., *Anuretes* Hell., *Gloiopotes* Stp. Ltk., *Lütkenia* Claus, *Nesippus* Hell., *Nogagus* Leach, *Demoleus* Hell., *Dysgamus* Stp. Ltk., *Euryphorus* Nordm., *Trebius* Kr., *Elytrophora* Gerst., *Alebion* Kr., *Dinematura* Latr., *Echthrogaleus* Stp. Ltk., *Cecrops* Leach, *Phyllophorus* Edw., *Gangliopus* Gerst., *Pandarus* Leach, *Laemargus* Kr., *Perissopus* Stp. Ltk., *Lepidopus* Dana., *Caligeria* Dana, *Calistes* Dana, *Caligina* Bened., *Speciligus*, Dana.

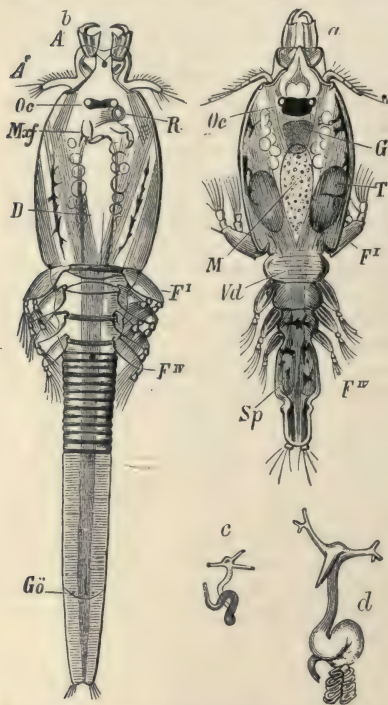


FIG. 266.—*Lernaea branchialis*. *a* male (about 2–3 mm. in length); *b* female at the stage in which fertilization occurs (5–6 mm. in length); *c* female in process of metamorphosis; *d* the same, with egg sacks formed (*c* and *d* natural size).

A, *A'* the two pairs of antennae (the hooked pair is the 2nd); *D* gut; *F*^I, *F*^{II} the four pairs of swimming feet; *G* brain; *Gö* region of the generative apertures; *M* stomach; *Mxf* maxilliped; *Oc* eye; *R* suctorial proboscis; *T* testes; *Vd* points to the vasa deferentia on their way from the testes to the genital (1st abdominal) segment. (After Claus.)

Nordm., *Aethon* Kr., *Ergasilina* Bened., and (?) *Polychinophilus* Hesse, and *Sabellacheres* Sars.

Fam. 14. **Lernaeidae**. Before they are fertilized the females (Fig. 266, *b*) resemble the males and conform to the type of the last two families, having the anterior antennae short, the posterior hooked and as in the last family projecting beyond the front margin of the

Fam. 13. **Dichelesthidae**.

Like the *Caligidae*, they are generally external parasites attached to the gills and soft parts of the skin of fishes. They differ from the *Caligidae* in the greater reduction in size of the swimming feet, the elongated body and in the characters of the antennae, the anterior being many jointed and the posterior, which are chelate or bear a hook, being lengthened so as to project beyond the margin of the cephalothorax. *Mytilicola* Steuer, *M. intestinalis*, internal parasite in gut of mussels in Adriatic; its blood is red. *Anthosoma* Leach., *Tucca* Kr., *Norion* Nordm., *Epachthes* Nordm., *Lernanthropus* Nordm., with red blood; *Stalagnus* Nordm., *Dichelesthium* Herm., *D. sturionis* on the gills of the sturgeon. *Lonchidium* Gerst., on the gills of sharks. *Baculus* Lub., probably a larval form of a Lernaeid allied to *Pennella*. *Philichthys* Stp., *P. xiphiae*. The sexes differ markedly in the adult state. The female inhabits the mucous canals in the head of the sword-fish (*Xiphias gladius*), but the male leads a free existence. *Lernaeascus* Claus, on soles. *Clavella* Oken, *Nemesis* Roux, *Cycnus* Edw., *Pseudocycnus* Hell., *Eudactylina* Bened., *Lamproglana* Nordm., *Donusa*

cephalothorax, the mouth parts suctorial, small hooked maxillipeds and four pairs of small swimming feet. The genital segment of the female is much elongated and the hind part of the body is unsegmented. A median eye is present throughout life. The development of the male ceases at this stage, but after fertilization the body of the female increases enormously in size, growing worm-like, while the anterior part is buried in the tissues of the animal on which it is parasitic (Fig. 266 c, d). The region in front of the genital segment is, in many genera, constricted, and the eggs sacs are either oval or much elongated, being in the latter case straight or thrown into a closely packed spiral. *Lernaeocera* Blainv., *Therodamas* Kr., *Peniculus* Nordm. *Pennella* Oken., *P. sagitta*, L. The female lives nearly buried in the flesh of the pelagic fish *Antennarius*, only the posterior part of the body carrying the straight egg tubes and beset on either side with a series of long processes (respiratory ?) projecting beyond the body of the host; two long backward pointing processes from the sides of the thoracic region anchor it in position. *P. filosa* L. attains a length of 6-7 inches. *Lernaeonema* Edw., *Lernaeenicus* Les., *Echetus* Kr., *Lophura* Köll., *Lernaeolophus* Hell., *Lernaea* L (Fig. 266). The females are parasitic on the gills of fishes (rarely on tunicates). The genital segment is swollen, ventricose and S-shaped. Rootlike processes extend from the head into the ulcerated tissues of the branchial arches in which it is embedded. The males remain small and lead a free life. *Haemobaphes* Stp. Ltk., *Peroderma* Hell., *Naobranchia* Hesse, and (?) *Pseudulus* Nordm.

Fifth series (Fams. 15-16).

Fam. 15. **Chondracanthidae.** The males and females differ much in form and size. The females are comparatively large animals attached to the gills or other soft parts of the skin of fishes. The abdomen is stump-like and the body produced into stout irregular processes (in which lobes of the ovaries may be lodged) giving it a monstrous misshapen appearance. There is no suctorial proboscis and the mandibles are sickle shaped. Maxillipeds small and hooked. The swimming feet are reduced to two pairs of bifid lobes. Egg sacs elongated or saccular. The dwarf males are found attached to the body of the female. In them the cephalothorax is arched dorsally and the abdomen conical and segmented. *Lesteira* Kr., *Medesicaste* Kr., *Strabax* Nordm., *Trichthacerus* Kr., *Blas* Kr., *Chondracanthus* la Roche (Fig. 265), *Splanchnotrophus* Hanc., *Diocus* Kr., *Ismailia* Bergh., *Tanypleurus* Stp. Ltk.

Fam. 16. **Lernaeopodidae.** As in the last family there is marked sexual dimorphism. The bodies of the females are large and unsegmented. Maxillipeds in some genera short and thick and in some cases completely fused together, but generally long and arm-like and only united at their ends in a single horny disc, common to both, by which the animal is attached to the host (Fig. 264). The toothed mandibles are contained in a suctorial proboscis. The swimming feet have completely disappeared. Egg sacks paired and saccular. The males resemble those of the Chondracanthidae in shape, but the abdomen is unsegmented, the mouth begins in a suctorial tube, and both second maxillae and maxillipeds are strongly hooked. They are attached to the bodies of the females. *Thysanote* Kr., *Basanistes* Nordm., *Vanbenedenia* Malm., *Charopinus* Kr., *Achtheres* Nordm., *Lernaeopoda* Kr., *Tracheliastes* Nordm., *Brachiella* Cuv.; *Anchorella* Cuv., on the gills and mouth parts of fishes (?) *Herpyllobius* Stp. Ltk.

Sixth series (Fam. 17).

Fam. 17. **Choniostomatidae.** Minute Copepods which live in the brood or branchial cavities or elsewhere about the bodies of different Malacostraca, whose blood they suck. The body, especially that of the fully developed female, is more or less globular, and without segmentation, though a transverse groove on the ventral surface marks the limit of the cephalothorax, and in one genus the abdomen is distinct. It is often partially clothed with hairs. The anterior antennae are small, the posterior very minute. Mandibles simple and contained in a conical proboscis terminating in a membranous cup. 1st maxillae minute and biramous, on the outer sides of the proboscis. The second maxillae and maxillipeds are generally powerful and prehensile. Two pairs of minute biramous legs and the pair of caudal appendages project from the globular posterior region. The male is often less than $\frac{1}{3}$ rd the length of the female and is attached to it or to the body of the host by a stalk secreted by a gland lying in front of the proboscis. The vasa deferentia open, according to Hansen, between the swimming legs of the anterior pair. The eggs are contained in numerous ovisacs which are generally not attached to the body of the female. A "nauplius" stage, though with only two pairs of appendages (cf. *Achtheres*, Lernaepodidae) is passed through in the egg and the larva is hatched in the "cyclops stage" with the mouth and anterior appendages like those of the adult, but with large swimming feet, and 1 or 2 free thoracic segments and a 3-jointed abdomen. The larvae attach themselves to a host by a secretion of the frontal border of the cephalothorax, and in some species either the female alone or both sexes pass through a pupal stage, in which the appendages are ill-developed or absent, and the contents of the body appears to undergo a process of histolysis. After the pupal skin is shed the adult structure is complete. *Stenothocheres* Hans., abdomen distinct, in marsupia of amphipod family Stenothoidae. *Homoeoscelis* Hans., in branchial cavity of Cumacea. *Sphaeronella* Salensky, in marsupia of amphipods, isopods and Cumacea, 34 spp. described. *Choniostoma* Hans., maxillipeds rudimentary; in branchial cavity of the decapod *Hippolyte*. *Mysidion* Hans., in marsupia of schizopods. *Aspidoecia* Giard and Bonn., attached to the outer surface of the schizopod *Erythrops*.

Sub-order 2. **BRANCHIURA.***

Carp-lice. Copepods with large compound eyes, and a suctorial tube about the mouth; with four pairs of elongated

* Jurine, Mémoire sur l'Argule foliacé, *Annales du Museum d'hist. nat.*, Tom. VII., 1806. Fr. Leydig, Ueber Argulus foliaceus, *Zeitschr für wiss. Zool.*, Tom. II., 1850. E. Cornalia, Sopra una nuova specie di crostacei sifonostomi, Milano, 1860. C. Claus, Ueber die Entwicklung, Organization und systematische Stellung der Arguliden, *Zeitschr. für wiss. Zool.*, Tom XXV., 1875. F. Leydig, Ueber Argulus foliaceus, *Arch. f. Mikrosk. Anat.*, T. 33, 1889. Nettovich L. v. Neue Beiträge zur Kenntniss d. Argulidae *Arb. aus dem Zool. Inst. Wien*. Bd. 13 (1900) p. 1. Wilson C. B., North American parasitic Copepods of the family Argulidae (with Bibliography) *Proc. U.S. Nat. Museum*, vol. 25 (1903) p. 635, and a new

biramous and many-jointed swimming feet. The abdomen is represented by a broad two-lobed caudal fin.

The *Branchiura* though actively swimming animals are parasitic on marine and freshwater fish. They are often placed near the *Caligidae*, but though they certainly resemble this group in the general form of the body they differ from them and from the *Eucopepoda* in several essential particulars.

They have an oval flattened shape enabling them to adhere closely to the bodies of their hosts. The region bearing the first pair of swimming feet is fused with the anterior part of the body forming a cephalothorax. The abdomen is represented by the short unjointed bilobed tail fin, in the notch at the end of which the short caudal furca is found (Fig. 267). Both pairs of antennae are small. The anterior is three-jointed and carries a hook and the posterior, though large and biramous in the larva, is simple in the adult. A large suctional tube projects from about the mouth, and in it are concealed finely serrated mandibles and the first maxillae which, unlike

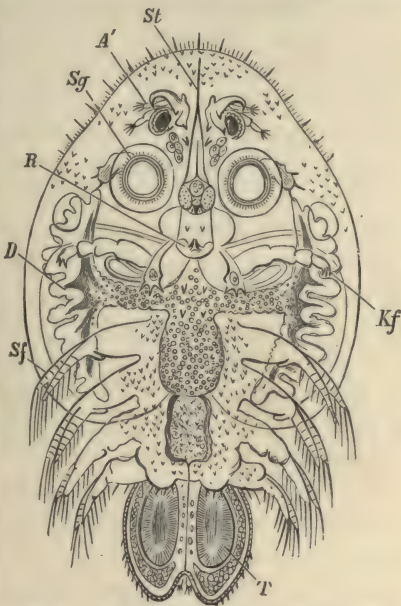


FIG. 267.—Young male of *Argulus foliaceus* (from Claus). *A'* Anterior antennae; *D* intestine; *Kf* maxilliped; *R* rostrum; *Sf* swimming feet; *Sg* sucker and second maxilla; *St* spine; *T* testes.

those of the parasitic *Eucopepods*, are styliform.* A little anterior to this proboscis there is inserted a long cylindrical tube, terminating in a retractile styliform spine, which serves as a sting (Wilson). It is, however, not present in *Dolops*.

species of *Argulus*. . . . *Ibid.* vol. 27 (1904) p. 627. Thiele J. Beit, z. Morphologie d. Argulidae. *Mitth. aus dem Zool. Mus. Berlin.* Bd. 2. Hft. 4 (1904).

* Thiele, however (l.c.), considers that only mandibles are contained in the suctional tube. He regards the appendages here named second maxillae and maxillipeds as the two pairs of maxillae—a result with which the position of the opening of the shell gland would be in harmony.

Powerful organs of attachment are placed on each side of and behind the mouth; they consist of two parts—(1) of an anterior pair of appendages which apparently correspond to the second maxillae and are in *Argulus* modified into large sucking discs; the hook-bearing terminal portion which is present in the newly hatched larva, and in *Dolops* throughout life, being reduced; and (2) of a posterior pair, which corresponds to the maxillipeds and is provided with numerous spines on its broad basal portion and a tactile protuberance and two curved terminal claws at its extremity. Next to these come the four paired swimming feet of the thoracic region, which, with the exception of the last, are, as a rule, covered by the sides of the cephalothoracic shield. Each of these consists of a large basal portion, consisting in the adult of several segments, and two much narrower rami, which are beset with long swimming setae and in their form and setigerous investment are not unlike the biramous appendages of the Cirripedia, being like them derived from the copepod feet of the larva (Fig. 267).

The internal organization recalls that of the Phyllopoda. The **nervous system** is distinguished by the great size of the cerebral ganglion, and by the close approximation of the six ganglia of the ventral chain. Two large compound lateral **eyes** are present in addition to the unpaired tri-lobed median eye. The **alimentary canal** consists of a short arched ascending oesophagus, a wide stomach with two lateral ramified appendages, and a rectum which runs directly backwards and opens to the exterior in the median indentation of the caudal fin above the two divisions of the caudal fork. The **shell gland** has a well-developed end-sac and opens, not as in most Entomostraca (but cf. footnote, p. 411) on the sucking disc (*mx''*), but at the base of the maxilliped. The **heart** is a tube suddenly expanded behind, extending from the region of the brain to the base of the caudal fin, against which it ends abruptly. The blood circulates in sinuses. It leaves the heart by anterior and posterior apertures and returns to it by a ventral median and two posterior lateral ostia (Leydig). The entire surface of the cephalothorax functions as a **respiratory** organ. There seems, however, always to be a strong current of blood in the caudal fin, so that this part of the body may be regarded as especially respiratory—a circumstance from which the group is named.

Reproduction.—The males are smaller and more agile than the females. The paired testes lie in the two lobes of the abdomen and the vasa efferentia lead to a median vesicula seminalis from which paired ducts pass to the median genital papilla at the base of the abdomen. Fertilization is effected by means of seminal sacs which are situated at the distal ends of the basal segments of the third pair of swimming feet, an arrangement recalling those found in spiders and cephalopods. Copulatory hooks are placed in a corresponding position on the fourth pair. The oviduct leading from the median ovary opens at the base of the abdomen. The females do not carry their eggs about in sacs in the typical copepod manner, but fasten them to surrounding objects. The vitelline membrane of the deposited eggs acquires a vesicular structure. The young when hatched have the general form of the adult, but the appendages, as shown by Claus, resemble those of later copepod larvae. They undergo a metamorphosis.

Fam. **Argulidae**, Carp-lice. *Argulus* O. Fr. Müll. The anterior pair of maxillipeds modified into large suckers. There is a styliform spine in front of the mouth. *A. foliaceus* L. (Pou de poissons, Baldner) parasitic on carp and sticklebacks. *A. coregoni* Thor., *A. giganteus* Luc., *Dolops* Aud. (= *Gyropeltis* Hell.). The maxillipeds end in a claw; styliiform spine absent. *D. Kollari* Hell., parasitic on the branchiae of *Hydrocyon*, Brazil. *D. Doradis* Corn. *Chonopeltis* Thiele.

Order 5. CIRRIPEDIA.*

Fixed, and for the most part hermaphrodite Crustacea with indistinctly segmented body enclosed by a dorsal shield (mantle) which generally contains calcareous shell plates. As a rule there are six pairs of biramous thoracic appendages. A remarkable change in the position of the body within the shell occurs in most cases during the metamorphosis.

* Compare J. V. Thompson, *Zoological Researches*, vol. 1, 1829. H. Burmeister, *Beiträge zur Naturgeschichte der Rankenfüssler*, 1832. Ch. Darwin, *A monograph of the Sub-Class Cirripedia*, 2 vols., London, 1851–1854. A. Krohn, *Die Entwicklung der Cirripeden*, *Archiv. für Naturgesch.*, 1860. C. Claus, *Die Cypris-ähnliche Larve der Cirripeden*, etc., *Schriften Ges. Naturw. Marburg*, Suppl. Heft. V. 1869. R. Kossman, *Suctorioria und Lepadina*, Würzburg, 1873. Yves Delage, *Evolution de la Sacculine*, *Arch. de Zool. exp.*, (2), II., 1884. Hoek, *Report on the Cirripedia*, Challenger Reports VIII (1883) and X (1884). Berndt, *Zur Biologie u. Anatomie v. Alcippe lampas Hancock*. *Z. f. w. Z.*, 74 (1903), p. 396. Gruvel, A., *Monographie des Cirrhipèdes*, Paris, 1905. G. Smith, *Rhizocephala, Fauna u. Flora d. Golfes von Neapel*, Monograph 29, 1906.

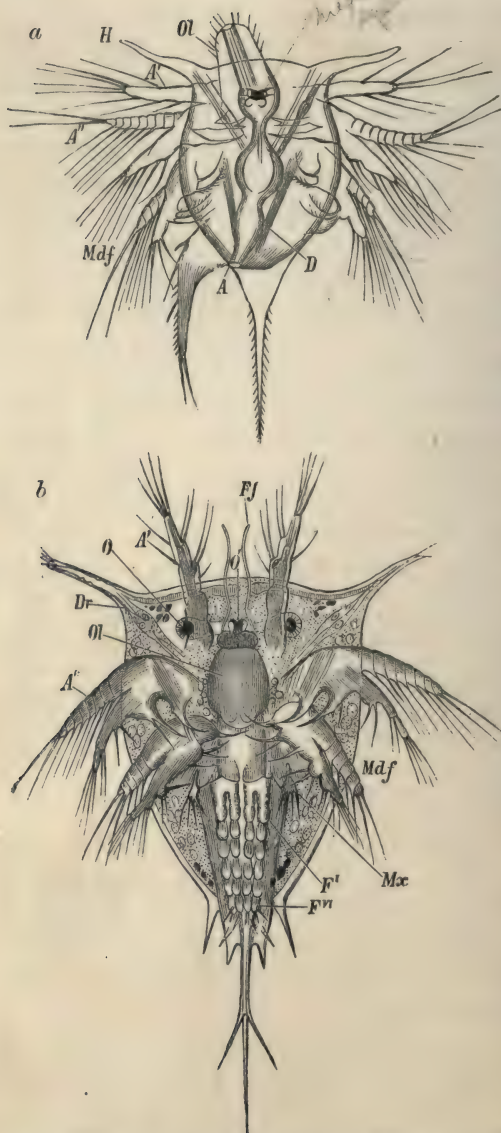


FIG. 268.—*a*, Late nauplius, *b*, metanauplius larva of *Balanus* before the moult. Beneath the skin are the rudiments of the lateral eyes (*O*) and all the appendages *F'* to *F''* of the cypris stage; *A* anus; *A'*, *A''* 1st and 2nd antennae; *A'* the antennae with suckorial disc; *D* intestine; *Dr* gland cells of the anterior horns; *Fj* frontal filament; *H* frontal horns; *Md* mandibular foot (third pair of appendages); *Mx* rudiment of maxilla; *O'* unpaired eye; *Ol* proboscis with mouth. (From Claus.)

The Cirripeds were included by the older naturalists in the Mollusca, to the Lamellibranch group of which the bivalve shell of the Lepadidae with its calcareous plates and the siphon-like peduncle give this division a certain external resemblance.

Their relationship to the Crustacea was first demonstrated by J. V. Thompson, by the discovery in the year 1829 of the nauplius larva of *Balanus*. The monograph of the Cirripedia by Charles Darwin (Ray Society 1851-53) first placed our knowledge of the structure of the group on a satisfactory basis.

The structure of the adult Cirripedes, as well as the natural affinities of the

group are best understood by the study of their development.

The nauplius larva (Fig. 268) is provided with the characteristic three pairs of appendages and median eye, but it also possesses a very delicate dorsal shield prolonged laterally into two peculiar "frontal horns" to which in the later stages, in *Lepas*, long median and lateral horns are added. The upper lip is large, recalling that of the Phyllopod larva.

After undergoing several moults in this guise the larva suddenly emerges in the **Cypris stage** (Fig. 269). It is enclosed in a bivalve shell, the margins of which are flattened along the ventral surface, and a pair of compound eyes is present in addition to the median eye. The anterior antennae are four-jointed, and bear a characteristic disc at the end of the second segment on which opens the duct of the cement gland, whose lobules lie in the anterior part of the body. The posterior antennae of the nauplius have disappeared, and the mandibles and two pairs

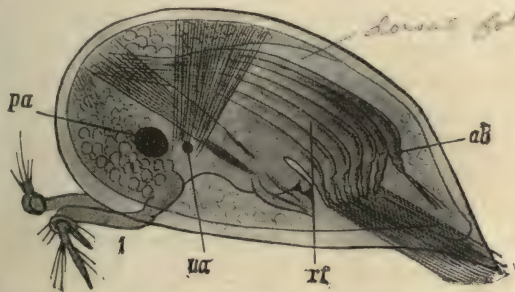


FIG. 269.—Cypris larva of *Lepas fasciculata*. *ab* abdomen; *pa* paired eye; *rf* thoracic feet; *ua* median (nauplius) eye, *1* anterior antennae. From Lang, after Claus.

of maxillae are rudimentary. There are six pairs of biramous and setose thoracic appendages, recalling those of Copepods. The short abdomen ends in a caudal fork. The position of the animal in relation to its shell is already peculiar. The mouth lies behind the middle of the ventral region and is directed backwards, so that, as shown in Fig. 269, the axis of the animal is bent into a **U** with unequal limbs. The fold where the inner lining of the carapace joins the dorsal body-wall, which we may call the *dorsal fold*, is situated on the dorsal side, and some of the soft parts are included in the fold of the carapace. The median eye lies a little behind the compound eyes, and at the bases of the antennae the chitinous covering forms two strong plates (apodemes) projecting deeply into the

body, for the attachment of the antennary muscles. They are indicated at a later stage in the plane of the paired eye in Fig. 270.

After a short time passed in the cypris stage, now swimming rapidly and now crawling by means of its leg-like antennae, the larva becomes fixed with the ventral margins of the shell applied to the object to which it is attached, and passes into the **pupal stage**.

The attachment is effected by the secretion of the cement glands by which the discs of the first antennae are glued on to the object selected by the larva for its resting-place. During this stage the compound eyes, the abdomen and other organs undergo a retrogressive metamorphosis, while the adult structures are developing. The curvature of the axis of the larva already marked, undergoes a considerable increase, the region bearing the mouth becoming directed still further backward (Fig. 270). In this marked flexure of the region of the body which lies about the alimentary canal, the anterior part, bearing the antennae and containing the cement gland, the compound eyes and the rudiments of the ovaries, does not participate. The result is that a partial separation of the body into two divisions is brought about; the space between the dorsal body wall and the carapace extends downwards (if we regard the ventral edge of the shell as horizontal, as in Fig. 269) and finally downwards and backwards, as it follows the curvature of the posterior region, until what we have called the dorsal fold (Fig. 271, *A* and *B*, *x*) comes to lie near the *ventral* surface of the larva.

When the pupal skin is shed the remains of the compound eyes, the larval swimming appendages and the above mentioned apodemes for the insertion of the antennary muscles are shed with it. As the result of the shedding of these chitinous plates a deep notch is left (Fig. 271, *B*, *y*) in the ventral side of the anterior end, lined but not filled by the delicate cuticle of the succeeding stage. The subsequent growth of this region is accompanied by a further change in the relative positions of the parts. The notch gradually opens out (Fig. 271, *C*), with the result that the part of the body posterior to it swings round through nearly a right angle, the ventral margin of the shell being now directed perpendicular to the surface of attachment, instead of parallel to it as heretofore.

The anterior part of the body becomes elongated in the Lepadidae into the stalk or peduncle and the ovaries and cement gland are contained in it. The antennae become shorter and

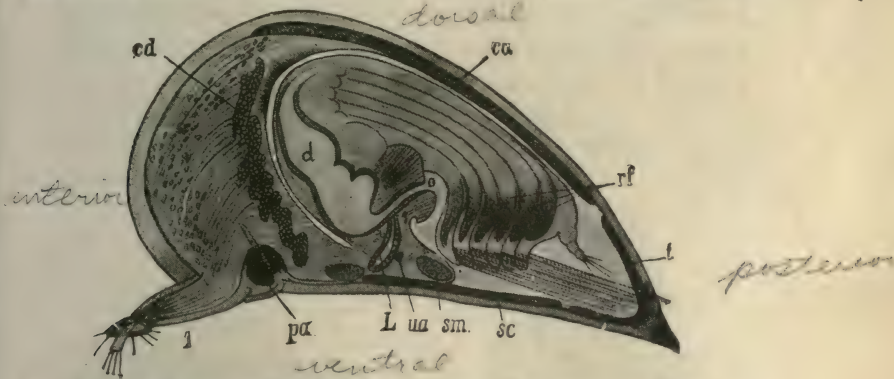


FIG. 270.—Pupa of *Lepas pectinata* in optical section. (From Lang, after Claus.) *ca* carina; *cd* cement gland; *d* intestine; *L* liver; *o* mouth; *pa* paired eye; *rf* thoracic appendages; *sc* scutum; *sm* adductor muscle; *t* tergum; *ua* nauplius eye; *l* anterior antennae.

stouter, and soon the region around them becomes flattened into a disc applied to the supporting object, though the com-

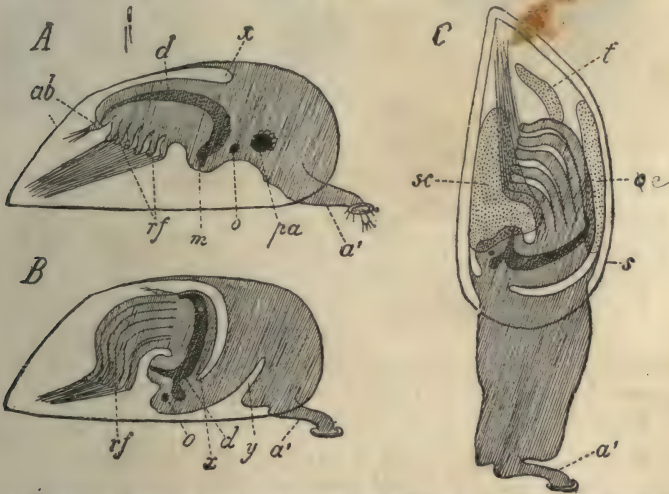


FIG. 271.—Diagrams illustrating the metamorphosis of *Lepas*. *A*, Cypris stage; *B*, attached pupa; *C*, young *Lepas* still surrounded by the loosened Cypris shell (*s*). *a'* first antenna; *ab* abdomen; *c* carina; *d* intestine; *m* mouth; *o* nauplius eye; *pa* paired eye; *rf* thoracic imbs; *s* Cypris shell; *sc* scutum; *t* tergum; *x* 'dorsal fold'; *y* ventral fold previously occupied by the apodemes of the antennary muscles (from Korschelt and Heider).

paratively minute antennae can be distinguished even in the full-grown barnacle.

In the Operculata or sessile barnacles the anterior part of the body does not undergo this elongation, but increases very largely in width, its "basis" or disc of attachment being the widest part of the body. In them the region of the body morphologically posterior is sunk in the wide anterior part, being surrounded by a fold of the outer wall (Fig. 272 *b*). Calcareous plates developed in this fold and in the wall of the anterior part below it constitute the *shell* or *testa*. The calcareous plates of the Operculata are described below, but it may here be pointed out that the

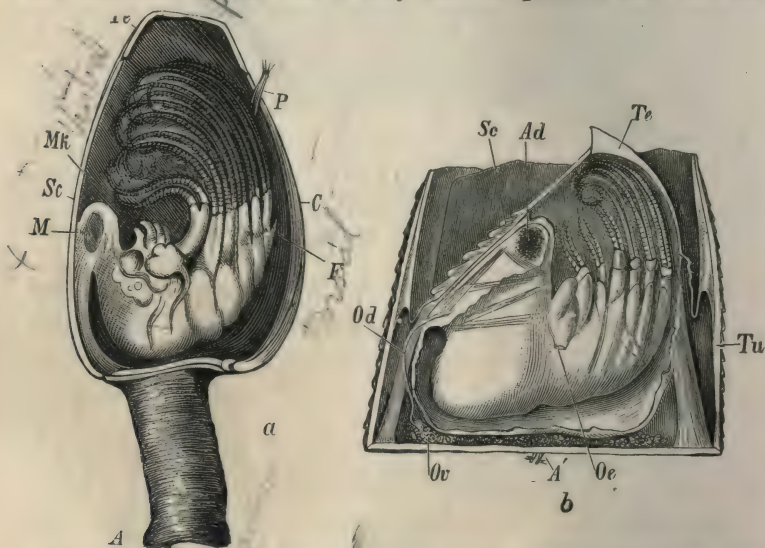


FIG. 272.—*a*, *Lepas* after removal of the right shell; *b*, *Balanus tintinnabulum* (after Ch. Darwin), one half of the shell has been removed. The following references apply to Fig. 272 *a* and *b*, and Fig. 273. *A'* anterior antennae at the end of the stalk in *a*; *Ad* adductor muscle; *C* carina; *Cd* Cement gland and duct; *Cf* thoracic appendages; *F* caudal fork; *L* liver; *M* muscle; *Mk* oral cone; *Od* oviduct; *Oe* opening of oviduct; *Ov* opary; *P* penis; *Sc* scutum; *T* testis; *Te* tergum; *Tu* section of the outer shell; *Vd* vas deferens. (After Claus.)

fold in question is distinct from that forming the mantle, being situated externally to it, and completely surrounding the body.

After the shedding of the bivalve shell of the pupa the fold of skin which supported it is covered by a thin cuticle in which however five local thickenings of chitin have already appeared. These are the provisional "valves" of the shell; they are always the first plates to appear, however many may be present in the adult shell, and in the Lepadidae the calcareous shells of the adult are formed under and about them.

The adult *Lepas*, whose relation to the larva may now be

understood (Figs. 272 and 273) is made up of the hollow muscular **peduncle** or stalk, containing the ovaries and the remains of the cement gland, and of the **capitulum**. The latter consists of the *mantle*, or dorsal shield, with its calcareous valves, together with the contained body, which is pear-shaped and formed, as we have seen, from part of the cephalic region of the larva, together with the thorax and rudimentary abdomen. The valves of the shell of the Lepadidae consist of a pair of large *scuta* (*Sc*) situated anteriorly, posterior and dorsal to them of a pair of *terga*, and of a single median and dorsal *carina* (*C*). The narrow end of the piriform body is divided by grooves into segments bearing the five posterior pairs of thoracic appendages. In front is the rounded and unsegmented *prosoma* bearing the first pair of thoracic and the oral appendages. It is connected with the mantle for a short distance in front of the mouth, and through this region passes transversely the great *adductor scutorum* muscle (Fig. 273, *M*).

Various modifications of the outer form of the body are met with. In *Conchoderma* the mantle remains to a large extent membranous, the valves being reduced in size. In *Anelasma*, which lives embedded in the skin of sharks, the valves are absent, and rootlike processes extend into the tissues of the host from the peduncle. The Pollicipedidae are transitional between the simple condition of *Lepas* and that presented by the Balanidae. In addition to five mantle plates homologous with those of *Lepas*, small calcareous plates are developed, in the cuticle of the peduncle, and larger accessory plates at the base of the capitulum. Among the latter a median ventral plate, the *rostrum*, is situated opposite to the dorsally placed *carina*.

In the Balanidae the carina together with the accessory (side) plates form the outer ring constituting the *testa* of this family. The carina, detached in this family from the true mantle, and the rostrum lie at either end of the median plane, and side plates are present in varying number (carino-lateral, lateral and rostrulo-lateral) overlapping one another at their sides. The *scuta* and *terga* on the other hand retain their position on the mantle covering the movable posterior part of the body, and together form the two halves of the

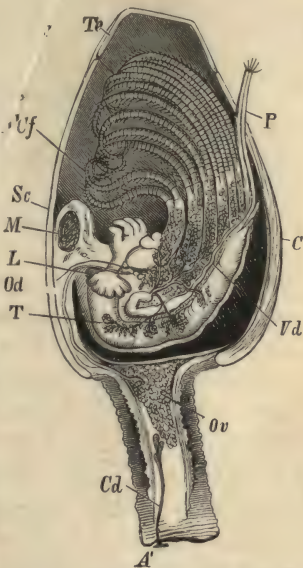


FIG. 273.—The organization of *Lepas*, after removal of the integument. (After Claus.) References as in Fig. 272.

operculum, which lies within the aperture of the testa, and when closed over the retracted thorax by the action of the *adductor scutorum* muscle forms a protection to the contained soft parts of the animal.

The remarkable departure from the symmetrical type presented by the *Verruidae* is described below.

The *mouth* opens on a prominent oral cone which projects backwards (Fig. 272, *M K*). In front is the large hood-like *labrum*, and at the sides are situated the toothed mandibles with their palps (Fig. 274), the toothed first maxillae, and the setose

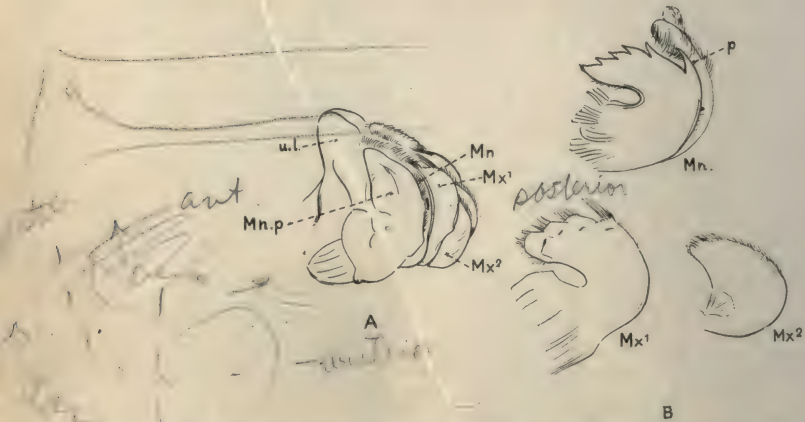


FIG. 274.—Mouth parts of *Lepas*. A seen from the right. B oral appendages of left side isolated and seen from the inner aspect; *Mn* mandible; *Mn. p* and *p* mandibular palp; *Mx*¹ 1st maxilla; *Mx*² 2nd maxilla; *u.l.* labrum.

swollen second maxillae which together limit the mouth cavity posteriorly. The six pairs of long, black, many-jointed, biramous, thoracic appendages (*cirri*) are curled towards the mouth, and richly beset with setae. With those of the opposite side they form a hand-like structure, which is rhythmically thrust out of the aperture of the mantle and swept through the water with a grasping motion, producing currents and capturing food. The *abdomen* has almost entirely disappeared, but from the ventral side of it there springs the long probosciform *penis*. A caudal fork represented by two short lobes is usually present in the *Pedunculata* and usually absent in the *Operculata*. In some genera of the former (*Alepas*, *Ibla* and *Lithotrya*), in the *Ascothoracica* and some *Acrothoracica* its lobes are longer and articulated. In *Lepas* two or more hollow processes situated near the bases of the anterior pair of thoracic feet are

regarded as branchial, and in *Conchoderma* a similar process is found at the base of each of the other thoracic feet. A fold of the inner lining of the mantle projecting backward on either side of the attachment of the prosoma to the carapace is the "*ovigerous frenum*" of the Lepadidae, and it is apparently a homologous structure, though no longer ovigerous, which is converted into a respiratory organ in the Operculata (Darwin).

The tubular *oesophagus* extends forward from the mouth to open into the dilated stomach, the walls of which are prolonged into *hepatic diverticula*. Bending with the curvature of the body the alimentary canal narrows into the intestine which runs back, in some cases with a clearly defined rectum, to open between the rudimentary abdomen and the base of the penis. In *Alcippe* it ends blindly.

Nervous system. A paired supra-oesophageal ganglion is present, and in the Lepadidae a ventral chain of five ganglia. In the Balanidae these latter are represented by a single large ganglion.

A vestige of the unpaired *eye* of the larva persists.

A *heart* appears to be absent.

The *excretory organs* are represented, as usual in Entomostraca, by the maxillary glands. Hoek described wide paired spaces, with definite walls, leading to apertures in the second maxillae. But it has recently been shown by Bruntz* that there are in addition glandular sacks (simple in *Balanus*, divided into alveoli in *Lepas*) lined by an excretory epithelium and opening into the spaces of Hoek, which are in fact their dilated ducts. Similar spaces are described by Berndt in *Alcippe*, but they are said to be closed.

Generative organs. In relation probably with their fixed habit the Cirripedes are almost exceptional among Crustacea in the fact that they are in the majority of cases hermaphrodite.

The *testes* (Fig. 273, T) are branched, glandular tubes lying at the sides of the alimentary canal and extending into the bases of the thoracic appendages. The *vasa deferentia*, after dilating at their commencement to form vesiculæ seminales, run back to unite at the base of the long penis, which is traversed by the common duct. The *spermatozoa* have a rounded head and

* Contrib. à l'étude de l'excrétion chez les Arthropodes. *Arch. de Biol. T. xx* (1904) p. 219.

long tail ending in two filaments. "Giant spermatozoa" have been observed, though rarely, in *Balanus perforatus*, by Gruvel.

The ovaries as already stated lie as a single mass in the peduncle of the Lepadidae, and in the corresponding basal region of the body in the Operculata. The paired oviducts open, not near the base of the abdomen, as usual in the Crustacea, but on prominences on the basal joints of the anterior pair of thoracic appendages. The eggs undergo their development in the mantle space, contained in two flattened gelatinous sacs, comparable to the ovisacs of the Copepods, which lie one on each side and are attached (in the Lepadidae) to the *ovigerous frena*. The mode of fertilization is described by Gruvel. In *Lepas* two individuals of a cluster come together, one of them, assuming the part of the male, deposits a viscous mass of spermatozoa on either side of the mantle cavity of the other, in the region of the orifice of the oviduct. The penis of a large individual may attain a length of 4-5 centimetres. A similar process has been observed in *Balanus*. Gruvel has observed self-fertilization to occur in an isolated specimen of *Pollicipes*.

The species of the genera *Ibla* and *Scalpellum* offer remarkable instances of sexual relationship. Most if not all are dimorphic; The species consists in some cases of hermaphrodite forms resembling those of allied genera of Lepadidae, but with certain dwarf male forms in addition, the "**complemental males.**" In other cases the two forms constituting the species are male and female the latter resembling the hermaphrodite forms of their allies, though without the male generative organs. In all, the male forms are small and are attached either in a pouch within the scutum or elsewhere about the mantle of the other form. They exhibit various degrees of arrested development and degeneration. Further details are given below.

The Acrothoracica are also dioecious, the males being degenerate and much reduced in size.

The Cirripedia are marine animals and attach themselves to various foreign objects. They are found fixed, usually in groups, to logs of wood, rocks, mussel shells, Crustacea, the skin of whales, Hydrozoan colonies, etc. Some as *Lithotrya*, *Alcippe* and the Acrothoracica, are able to bore into the shells of Molluscs and Corals.

The members of the sub-orders Apoda, Rhizocephala and

Ascothoracica are parasitic. The relations between the Rhizocephala and their Crustacean hosts are among the most astonishing examples of parasitism to be found in natural history.

The Lepadidae are represented in Ordovician strata by examples of the Pollicipedidae (including the existing genus *Pollicipes*) and attain their culminating point during the Cretaceous period. The curious unsymmetrical Verrucidae appear in the Cretaceous, but the other groups of Operculata are not known prior to the Tertiary period.

Sub-order 1. CIRRIPEDIA GENUINA.

Tribe 1. **PEDUNCULATA.** Body stalked, with six pairs of biramous feet. *Scuta*, *terga* and a *carina* are usually formed on the mantle, and when other plates are present they are not united into an immovable ring.

Fam. 1. **Lepadidae.** The stalk is sharply marked off from the capitulum, and calcareous plates are not developed on it. The plates on the capitulum are thin, their number does not usually exceed five, and the terga lie *behind* the scuta. Hermaphrodite. *Lepas* L. (Figs. 272 and 273) attached to floating objects; *L. anatifera* L., like most of the species of the genus, cosmopolitan, from arctic to tropical seas. *Megalasma* Hoek, *Poecilasma* Darw., generally attached to crustacea. *Oxynaspis* Darw., *Dichelaspis* Darw., the calcareous plates on the mantle are separated from one another by wide intervals, and the scuta and terga are deeply notched; they live attached to sea-snakes or crabs. *Conchoderma* Olfers, capitulum in the main membranous, the plates are small and may be reduced to two (scuta). Cosmopolitan, attached to floating objects, living or inorganic. *Alepas* Rang., capitulum without plates, or with horny almost hidden scuta; attached to various floating objects; *A. parasita* Rang. on medusae. *Anelasma* Darw., *A. squalicola* Lovén, the peduncle is embedded in the skin of the sharks *Squalus maximus* and *Spinax* living in the North Sea, the skin of the cirripede being produced into branching rootlike processes, knobbed at their ends, which ramify in the tissues of the fish. The capitulum is without plates and has a wide aperture. The six pairs of legs have a shapeless appearance; they are obscurely articulated and without setae. *Gymnolepas* Auriv., pelagic, on medusae; cirri articulated and setose. *Chaetolepas* Studer, on sertularians.

Fam. 2. **Pollicipedidae.** The stalk usually obscurely divided from the capitulum, and covered with calcareous scales or chitinous hairs. Capitulum with numerous massive plates, frequently exceeding five in number; the terga are rather *dorsal* than posterior to the scuta. Many species are hermaphrodite, some with complemental males, and some are dioecious. *Pollicipes* Leach, stalk closely covered with scales or spines; in addition to the five plates of the Lepadidae, rostral and lateral plates are strongly developed, and many smaller additional plates (18 to 100 or more) clothe the base of the capitulum; hermaphrodite; attached to fixed or floating objects in the warmer seas of the globe. *P. signatus* Aur., occurs in Silurian of the I. of Wisby in the Baltic.

Lithotrya Sow., with an elongated peduncle covered with scales, and eight plates on the capitulum; the body is sunk in the cavity of the peduncle; the animal lives in deep burrows which it excavates in calcareous rocks, corals or shells; tropical, hermaphrodite. *Ibla* Leach, attached to littoral objects in the warm seas of the eastern hemisphere. *I. Cumingii* Darw. Contrary to the general rule among cirripedes the sexes are separate and exhibit marked dimorphism. In the *female* the scuta and terga only are developed and they are not calcareous but horny. The peduncle is covered with spines, and the body is partly sunk within its cavity. The first pair of cirri is separated by a considerable interval from the remainder. The *males* are minute degenerate creatures, and one or more are attached within the mantle cavity of the female. The capitulum is almost undeveloped, but the peduncle is comparatively large and tapers to a point, which is embedded in the tissues of the female and bears the characteristic prehensile antennae. The mouth parts are well developed and a complete alimentary canal is present, but the thoracic appendages are reduced to two pairs, apparently the 5th and 6th, and these are small and irregular. There are well developed testes and vesiculae seminales but no penis. Philippines and Burmah, attached in groups to the peduncles of *Pollicipes mitella*. The other species, *I. quadrivalvis* (Cuv.), from the Australian seas, consists of hermaphrodite forms and "*complemental males*." The hermaphrodite forms resemble the female of *I. cumingii* except that, like most Cirripedes, they possess the male reproductive organs in addition to the female. The males also resemble those of the other species except that there are a distinct penis and a caudal fork the halves of which are divided into three segments. The caudal appendages of the hermaphrodite form are remarkably long. *Scalpellum* Leach, presents similar remarkable instances of sexual relations. In the *hermaphrodite* or *female* form there are 12-15 calcareous plates on the capitulum and the peduncle is nearly always squamiferous. In all the living species that were known when Darwin wrote his monograph, small *male* forms are attached to the number of two or more about the body of the other form. In some cases these are distinctly pedunculated, the capitulum carries calcareous plates, and an alimentary canal and 6 pairs of cirri are present. In *S. ornatum* and *S. vulgare* however the males are reduced to flask-shaped bodies, without an alimentary canal, with 4 minute calcareous plates, and only four pairs of cirri which are nonprehensile. In others again the valves have completely disappeared. They always however retain the characteristic cirripede antennae, by which they are attached. The more degenerate males are contained in small pocket-like cavities on the inner surfaces of the scuta of the other form, they are without a functional alimentary canal and it is probable that many of these short-lived forms successively occupy the scutal pouches. In *S. ornatum* the larger form is, according to Darwin, female, and this may be the case in one other species, but in *S. vulgare*, *rostratum*, *peronii* and *villosum* the larger form is hermaphrodite, although, possibly in relation to the presence of the complemental males, the male system of the hermaphrodite form is in some cases under-developed. The species are found attached to the slender branches of hydrozoan colonies. *S. vulgare*, British and adjacent coasts. Many species are found in the deep sea (over 2,000 fms.). Among 41 new species of *Scalpellum* in the "Challenger" collections (about half of them represented by a single specimen), Hoek found the reduced

male in 19, confirming the results which Darwin arrived at on much more meagre material.

Tribe 2. **OPERCULATA.** The peduncle is rudimentary or absent. The body is surrounded by a ring of plates (*testa*) the entrance to which can be closed by the *scuta* and *terga* which together form an operculum and (except in *Verrucidae*) are provided with depressor muscles.

Fam. 1. **Coronulidae.** Scuta and terga when present freely movable, but not articulating together. Rostrum overlapping the adjacent plates laterally. Base of the shell membranous. The paired branchiae each consist of two folds. On cetacea and other pelagic vertebrates. *Coronula* Lam., attached to the skins of cetacea. Testa not so high as it is broad; it consists of 6 similar broad pieces of shell the walls of which are thin and deeply folded, the cavities of the folds are turned towards and are filled by the epidermis of the host; terga and scuta small, not filling the aperture of the testa; three species. *Platylepas* Gray, resembling *Coronula*, but the pieces of the shell are bilobed; in the warmer seas, attached to turtles, sea-snakes and manatee. *Tubicinella* Lam., testa much higher than it is broad, formed of six amalgamated pieces; these basket-like cirripedes are embedded in the skins of whales in the S. Ocean, often associated with *Coronula balaenaris*. *Stephanolepas* Fischer, on *Chelone imbricata*. *Xenobalanus* Steenstr., shell a shallow six-rayed ring embedded in the superficial layers of the skin of the porpoise on which this cirripede lives; the body is much elongated (nearly 2 inches), and externally resembles one of the Pedunculata, only the base of it being contained in the shell; it consists however of the elongated mantle the cavity of which extends down to the cavity of the shell; the margins of the aperture are reflexed forming a collar, and there are no shell plates; N. Atlantic.

Fam. 2. **Balanidae.** Scuta and terga freely movable, and articulating with one another. The paired branchiae each consist of a single fold with subordinate lateral folds. *Balanus* Lister, testa cylindrical or conical, consisting of 6 pieces; from the upper limit of the tidal zone to 50 fms., in arctic to tropical seas throughout the world; 41 species. *Acasta* Leach, lives attached to sponges. *Tetracita* Schum., testa composed of four pieces (carina, rostrum and 2 lateral) permeated by pores; *T. porosa* Gmel., the number of segments in the cirri is very variable. *Elminius* Leach, testa composed of four pieces not porous. *Pyrgoma* Leach, testa formed of a single piece; the scutum and tergum of each side are more or less completely joined together. Lives embedded in corals, chiefly in tropical seas. *Creusia* Leach, like *Pyrgoma*, but the testa consists of four pieces. *Chelonobia* Leach, testa of 6 pieces, one of them consisting of the rostrum and two rostro-lateral elements united together. The pieces are thick-walled and not infolded from the base; scuta narrow united to the terga by a horny articulation; attached to turtles, crustacea and smooth gastropod shells, throughout the warmer and tropical seas.

Fam. 3. **Chthamalidae.** Rostrum overlapped laterally by the adjacent plates. *Chthamalus* Ranz., *Chamaesipho* Darw., *Rachylasma* Darw. found in deep water. *Octomeris* Sow., testa formed of 8 pieces. *Catophragmus* Sow., testa formed of 8 large pieces, with imbricated series of smaller plates set round about them, becoming smaller towards the base. Littoral; W. Indies and Australia.

Fam. 4. **Verrucidae.** Scuta and terga without depressor muscles. Those of one side only (right or left) move freely, their fellows having

coalesced with the carina and rostrum to form one unsymmetrical ring of 4 plates, resembling the testa of other Operculata. The four species of the genus *Verruca* which constitute the living representatives of this family present a remarkable departure from the bilateral symmetry characteristic of other Cirripedes. Superficially the shell appears to be formed on the same plan as in other Operculata, but the operculum which lies in the aperture of the shell is formed of the scutum and tergum of one side only, those of the other side having taken their places in the outer wall of the shell, which is completed by the carina and rostrum. The prehensile antennae of the larva are situated at about the middle of the (membranous) basis of the shell, but the body of the animal, which is symmetrical about its own median plane, lies on its side, with that plane parallel to the surface of attachment. The early larval stages are symmetrical and the terga and scuta of opposite sides are alike at their first formation. The lobes of the caudal fork are unusually long. The shape, mode of growth and articulation of the tergum and scutum show affinities with the *Lepadidae*. The shells are generally attached to living bodies and are found down to a depth of 90 fathoms, from Iceland to Cape Horn. *V. strömia* (O. Müll.) is British. A fossil species is found in the Chalk.

Sub-order 2. ACROTHORACICA.

Minute Cirripedes of separate sexes. The *females* are enclosed in a flask-shaped mantle beset with chitinous points and live in hollows which they excavate in the shells of Molluscs. The thoracic appendages of the first pair are palpiform or rudimentary, and two to four pairs of cirriform feet are borne at the posterior end of the body. The intermediate appendages are absent. Mouth parts and alimentary canal usually well developed (the latter ends blindly in *Alcippe*). The males where known are dwarfed, without alimentary canal, and spend their short existence attached to the mantle of the female.

The genus *Cryptophialus* was placed in a distinct order of Cirripedes, the Abdominalia, by Darwin on the indication afforded by the apparent segmentation of the body. As seven segments appear to intervene between that bearing the maxillipeds (first thoracic) and the region from which the three pairs of biramous appendages, at the posterior end of the body, arise, it seemed evident that the latter could not be homologous with the 4th, 5th and 6th thoracic appendages of other Cirripedes. There are however reasons for not regarding the apparent segments as indicative of the true segmentation. The disc by which the adult is attached to its burrow must include, at its anterior end, the region from which the first antennae of the pupa sprang (the 1st antennary segment); yet the disc is borne on the apparent segment posterior to that bearing the maxillipeds together with the other oral appendages. Hence, in the anterior part, the apparent is no guide to the true segmentation.* The close resemblance between *Cryptophialus* and *Alcippe* was fully recognized by Darwin, and the subsequent discovery of *Lithoglyptes* and *Kochlorine*

* The same argument applies to *Proteolepas*, the representative of the following sub-order. In it the larval antennae persist throughout life, and are borne behind the mouth on the second ring as indicated by the superficial appearance of segmentation.

link these genera even more closely together. In them, as in *Alcippe* there is no appearance of the segmentation of the anterior part of the body indicated in *Cryptophialus*. If we disregard this apparent segmentation, the four genera fall into a natural group for which the name Abdominalia becomes misleading and for which Gruvel has proposed the name Acrothoracica, in allusion to the fact that the terminal feet are confined to more or fewer of the apical (terminal) segments of the thorax.

The group so formed has affinities, as pointed out by Darwin in the case of *Alcippe*, with the *Lepadidae*. There are however indications that they belong to a more generalized type than any of the Thoracica. If we take the oral end of the disc of attachment as representing the region of the 1st antennary segment, there is no such wide separation of the mouth from this region as occurs in that group. Hence the relations of

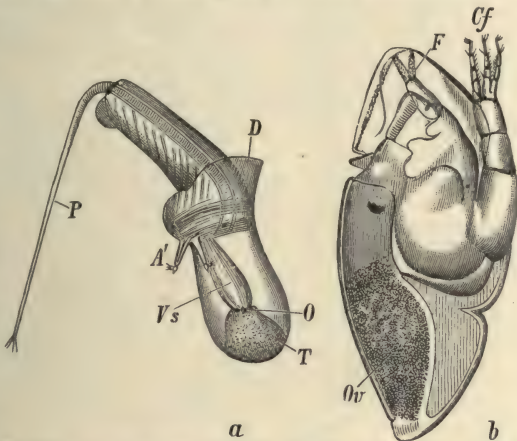


FIG. 275.—*Alcippe lampas* (after Ch. Darwin). *a*, male, very strongly magnified; *b*, longitudinal section through female. *A'* the right antenna (the left is seen through the transparent body); *Cf* three posterior pairs of appendages; *D* lobe of the mantle; *F* maxilliped (first thoracic appendage); *O* eye; *Ov* ovary; *P* penis, projecting from the orifice of the flask-shaped mantle cavity, at the lower (anterior) end of which is situated *T* the testis; *Vs* seminal vesicle. The thickened band to the left of *Ov* is the section of the large disc by which *Alcippe* is attached to the wall of its burrow.

with *Lithotrya*, *Ibla* and *Alepas* among the Pedunculata. Berndt * has recently brought evidence to show that the appendages which have been regarded as the caudal fork in *Alcippe* are the 6th pair of thoracic appendages.

Fam. 1. **Alcippidae.** The females (Fig. 275 *b*) live in hollows in the columella of the shells of *Fusus* and *Buccinum* (British) to the wall of which they are attached by a large horny disc, the plane of which is parallel with that of the orifice of the burrow. Their position in relation to the surface of attachment is the same as that of the pupa of *Lepas* (cf. Figs. 270 and 275). First pair of thoracic appendages large and palpiform, and the three posterior appendages uniramous. They probably

* *Zeits. für wiss. Zool.*, Bd. 74, p. 396.

represent the 4th, 5th and 6th thoracic appendages (the 2nd and 3rd being absent). The dwarf males (Fig. 275, *a*) are without alimentary canal and hence are short-lived, and have a long probosciform penis. Several may be found in the neighbourhood of the upper part of the disc. *Alcippe* Hanc. *A. lampas*.

Fam. 2. **Lithoglyptidae**. 3 spp. of the single genus *Lithoglyptes* Aur. have been described by Aurivillius, living in burrows which they excavate in coral or in the shells of molluscs. There are 5 pairs of thoracic appendages the 2nd only being absent, and 3-4 jointed caudal appendages. The plane of the disc of attachment is nearly at right angles to that of the orifice of the burrow. Alimentary canal complete. E. Indies.

Fam. 3. **Cryptophialidae**. Three pairs of biramous cirriform feet at the posterior end of the body. *Cryptophialus* Darw., *C. minutus* Darw. The female attached by a disc, as in *Alcippe*, in the shell of the gasteropod *Concholepas peruviana*; W. coast of S. America. There appear to be 10 post-cephalic segments of the body. The anterior thoracic appendages rudimentary. Alimentary canal complete. The dwarf males resemble those of *Alcippe*.

Fam. 4. **Kochlorinidae**, contains the single genus *Kochlorine* Noll., *K. hamata* Noll.* in the shells of *Haliotis* and other molluscs, at Cadiz. Female attached to the edge of its burrow by hooks only. The body not definitely segmented; anterior thoracic appendages large and palpiform, as in *Alcippe*. Behind the large cirriform feet is a pair of jointed caudal appendages. Males not certainly known.

Sub-order 3. **APODA.**

With the characters of the family.

Fam. **Proteolepadidae**. *Proteolepas bivineta* Darwin, the sole representative of this sub-order is a small maggot-like animal about $\frac{1}{4}$ th of an inch long, which lives attached by its antennae in the mantle cavity of the pedunculate cirripede *Alepas cornutus*. The antennae have the characteristic Cirripede shape, but the mantle and all appendages, except those of the mouth, are absent, and the body is divided, by constrictions, into 11 rings, which however, in view of the facts that the mouth, with its 3 pairs of appendages, is borne on the first body ring, and the antennae on the second, cannot be regarded as representing primary segments. It is hermaphrodite and the body is mainly occupied by the largely developed ovaries. The mouth is suctorial and the alimentary canal ends blindly. St. Vincent, W. Indies.

Sub-order 4. **RHIZOCEPHALA.** †

The Rhizocephala are parasites on Malacostracan, and mainly on Decapod Crustacea. In the adult state they con-

* Noll. F. C., *Kochlorine hamata* N. ein bohrendes Cirriped. *Zeits. f. Wiss. Zool.*, Bd. 25 (1874-5), p. 114.

† W. Lilljeborg, Les genres *Liriope* et *Peltogaster*, *Nova Acta. reg. soc. scient.*, Upsala, Ser. 3, vol. iii., 1860. Fr. Müller, Die Rhizocephaliden, *Arch. für Naturgesch.*, 1862 and 1863. R. Kossmann, Beiträge zur Anatomie der schmarotzenden Rankenfüssler, *Verhandl. der med.-phys. Gesellsch. Würzburg*, Neue Folge, Tom. IV. Yves Delage, Evolution de la Sacculine, *Arch. de Zool. Exp.*, 2 Sér., Tom. II., 1884. Smith, G., Rhizocephala, *Fauna u. Flora d. Golfes von Neapel.*, Monog. 29 (1906).

sist of a swollen body, which projects from the host through an aperture on the ventral surface, and of a system of roots which ramify through the tissues of the host (Fig. 277). As in the case of the Cirripedia Genuina the structure of the adult is best elucidated by the study of development.



FIG. 276.—Consecutive larval stages of *Sacculina carcini* (from Lang, after Delage). A, nauplius after first moult; B, free swimming Cypris-stage; C, Cypris-stage after the larva has become attached to a seta (bb) of the host; D, formation of the Kentrogon larva; E, the Kentrogon larva after the Cypris shell has been thrown off and the pointed process formed; F, the process has pierced the cuticle of the host.

1, 2, 3 the nauplius limbs; I-VI the thoracic limbs of the Cypris stage; ab abdomen; bb seta of the host; f fat globules; fs frontal sensory organ; gl glands of the frontal horns; ov rudiment of the ovary; pf pointed process; ua nauplius eye.

Much light has been thrown on the structure and life-history of this group by the admirable researches of Yves Delage on *Sacculina carcini* Thomps. In the nauplius larva (Fig. 276, A) the mouth and alimentary canal are absent, but a mass of "primitive ova" can already be distinguished. In the Cypris stage the antennae are prehensile and bear two large sense organs, and the 6 pairs of biramous swimming legs are well developed. After swimming freely for two or three days the larva attaches

itself to a young crab, most frequently (in the neighbourhood of Roscoff, where Delage carried on his researches) to *Carcinus moenas*.

The larva grasps the base of one of the crab's setae with one of its antennae, and there remains attached (Fig. 276, *C*). The whole of the posterior parts of the body of the larva including the swimming appendages and their muscles, together with the eye, ganglion and excretory organs now break down and are shed by rupture of the ectoderm. There remain the ectoderm, which is rapidly made whole, the mass of primitive

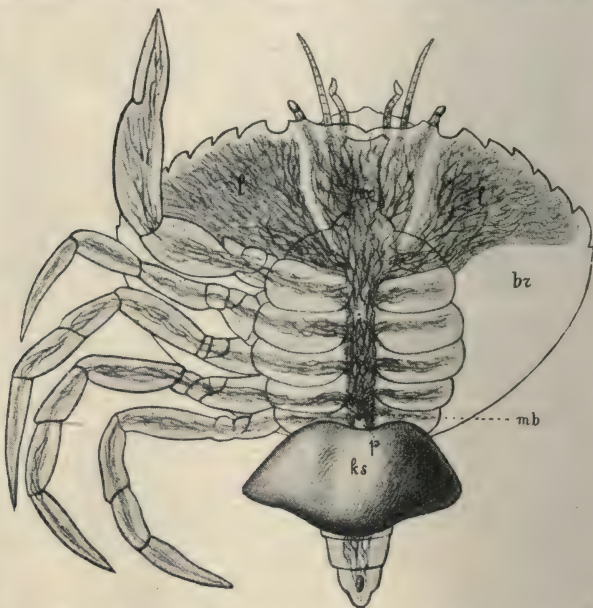


FIG. 277.—*Sacculina carcini* in situ on the host (from Lang after a diagrammatic drawing by Delage). *br* branchial, *d* intestinal and *l* hepatic regions of the crab. *ks* the body and *p* the pedicle of the *Sacculina* (external); *mb* basilar membrane from which the roots of the parasite proceed throughout the body.

ova and a small number of other mesoblastic cells (Fig. 276, *D*, *E*). The bivalve shell of the Cypris stage is also shed, but the antenna remains connected at its base with the new cuticle secreted by the ectoderm, and still holding on to the seta. This process is completed in about 3 hours. The soft-parts now shrink away from the anterior part of the old cuticle and form a new one within it. The new cuticle is produced in front into a pointed process open at the end, and behind is invaginated around the base of the process (Fig. 276, *E*). At this stage the young Cirripede is known as the *Kentrogon larva*. As growth proceeds the base of the process becomes evaginated, with the result that its point is thrust forward along the hollow antenna (Fig. 276 *F*) and pierces the soft cuticle of the crab at the base of the seta to which the larva is attached. The soft parts of the larva, consisting of the mass of primitive ova and other mesoblast cells, surrounded by a layer of ectoderm, now travel along the hollow process of the cuticle and enter the body of the crab.

At the stage at which this remarkable Cirripede can next be recognized it has taken up its position in the connective tissue of its host between the intestine and the muscles lying in the ventral wall of the abdomen.* The *internal Sacculina*, as it is now called, consists of a rounded mass of cells, containing a minute compact body, the primitive ova, and continued at its edges into long root-like processes which ramify throughout

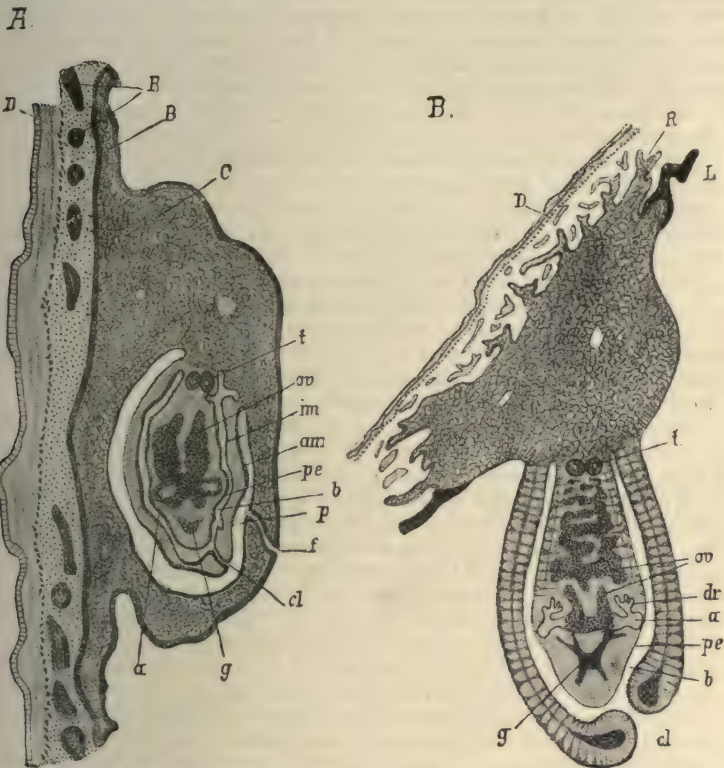


FIG. 278.—Longitudinal sections through two stages of development of *Sacculina carcini* (from Korschelt and Heider after Delage). *A* *Sacculina interna*; *B* *Sacculina externa*; *a* atrium (widening of the oviduct); *am* outer mantle layer; *b* brood-cavity (mantle cavity); *B* basal membrane; *C* central tumour; *cl* cloacal opening; *D* intestinal wall of host; *dr* cement glands of the ovarian sac; *f* aperture of the perivisceral cavity; *g* ganglion; *im* inner mantle layer; *L* body-wall of host; *ov* ovary; *p* perivisceral cavity; *pe* perivisceral ectodermal layer; *R* root processes (some in cross section); *t* rudiment of testes.

the soft tissues of the host, even to the tips of the extremities. The crab's heart and branchiae alone are free from the ramifications of its parasite (Fig. 277). As the central mass slowly grows, it begins in time to press against the ventral wall of the abdomen of the crab, which softens and

* Mr. G. Smith has recently recognized the parasite when it formed a mass not more than 2 mm. in diameter, and lay considerably in front of its final position.

gives way before it. Through the aperture so produced the body of the parasite projects into the outer world (Figs. 277 and 278, B).

The *Sacculina* now enters on its final phase of existence in which it is known as the *external Sacculina*. It forms a flattened oval mass about the size of the terminal joint of the little finger, whose long axis is transverse to that of the abdomen. It is connected with its host by a short pedicle which passes from one end of the shorter axis through the abdominal wall, and is continued into the system of roots (cf. Fig. 278, B). At the opposite end of the short axis from the pedicle is the *cloaca*, which, until a brood of young has been produced, is closed by a chitinous plate projecting at the sides, beyond the lips of the cloaca. This leads into the *brood-chamber* (Fig. 278, B, b) surrounding a central *visceral mass* which projects from the region of the pedicle into it. The wall bounding the brood-chamber externally is known as the *mantle*. It is connected with the visceral mass by a mesentery which is of small breadth but extends from the region of the pedicle nearly to the cloaca along the side which is turned towards the right side of the crab. The *Sacculina* thus lies in a definite relation to its host. In the visceral mass lie the large paired *cement glands* (*dr*) and open on either flattened face (Fig. 278 B). Near its base lie two cylindrical *testes*. The vasa deferentia open into the brood chamber. A *ganglion* is situate on one side of the plane of the mesentery in the visceral mass and supplies nerves to it and to the mantle, which they reach through the mesentery.

According to Delage's view all but the first batch of eggs are fertilized by the spermatozoa of the animal which produces them, and this is effected before the ova leave the oviducts; the spermatozoa finding their way into the latter from the brood-chamber. When a batch of eggs is ripe the cuticular lining of each of the cement glands is shed all in one piece, and the multilobed digitate bag so produced becomes distended with the eggs in its passage to the brood-chamber. The two batches of eggs each contained in its cuticular sack, lie in the brood-chamber on either face of the flattened visceral mass. They are held in position by minute hooked prominences (*retinacula*) which project from the inner lining of the brood-chamber, and are supplied with oxygen by the regular contraction of the mantle. From the eggs emerge the nauplius larvae above described.

It appears that no very long time elapses between the entry of the parasite into the crab and its taking up its position under the gut. According to Delage the *Sacculina* becomes *external* at the age of 20-22 months, the host being about four months older. The first brood is produced four months later, and other broods succeed, during the summer at intervals of 4 or 5 weeks. A *Sacculina* becomes external and begins to produce broods in the late summer, and the production of broods is continued during the next summer. At the end of this second summer, being aged rather more than three years, it dies. While the *Sacculina* is external and producing its broods of nauplii the drain on the resources of the host is greatest, and the Crab does not increase in size or moult though it is not necessarily prevented from producing its own young.*

* In the case of the crab *Inachus* which is infested by a species of *Sacculina*, permanent infertility results from the action of the parasite. Cf. p. 445.

The effect of the presence of the parasite on the host is referred to on p. 445.

It remains to notice the fact that when the *Sacculina* has become external, but before the plate of chitin has disappeared from the cloacal opening, numbers of *Cypris* larvae are found to attach themselves by their antennae in the angle between the mantle and the projecting edge of the plate covering the cloacal opening. These have not been seen alive and nothing is known of their internal structure beyond the fact that they do not shed their swimming appendages or develop the pointed process of the cuticle formed by larvae which attach themselves as parasites. It is conjectured that these larvae are males, which in some way, at present unknown, fertilize the first batches of ova.

The name *Rhizocephala* and the term "mantle" as above used imply definite homologies with the parts of other Cirripedes, and the question arises, How far is the use of these terms justified? Notwithstanding the complexity of the metamorphosis undergone by these remarkable Cirripedes there appears to be nothing in the life-history to render untenable the view that there exist in the fully formed *Sacculina* parts corresponding to the mantle and the head region of other forms.

With regard to the mantle, its relation to the visceral mass bears no doubt a certain resemblance to the relation of the mantle fold of other Cirripedes to the contained body; but the account which Delage gives of the origin of the layers lining the brood-chamber, by *delamination* from an outer epithelial layer, lends no support to this homology. The ganglion, again, is formed as an ingrowth from this same outer layer, not in the plane of the mesentery but on one side.

It must be confessed that the homology of the "mantle" of the *Rhizocephala* with that of other Cirripedes is uncertain; and if this is uncertain there is no satisfactory reason for regarding the pedicle and the region from which the roots spring as anterior.

The name *Rhizocephala* therefore, though retained here as that by which the group is usually known, implies a view of the homologies of the adult structure which is at least insecure.

The *Rhizocephala*, parasites of other Crustacea, are themselves liable to be infested by members of the *Epicarida*, a parasitic group of the *Isopoda*.

Fam. *Rhizocephalidae*. Degenerate Cirripedes, parasitic on Crustacea, and undergoing a remarkable metamorphosis. *Peltogaster* Rathke, irregularly cylindrical, uncompressed; cloacal opening anterior in relation to host; on Decapoda Anomala. *Parthenopea* Kossmann, roughly spherical, mantle opening lateral; on *Callianassa* and *Gebia*. *Sacculina* Thompson, much compressed laterally, cloacal opening posterior, on Decapoda Brachyura. *Heterosaccus* G. Smith, like *Sacculina*, but with the mantle opening widely gaping; on Decapoda Brachyura. *Lernaeodiscus* Müller, mantle expanded laterally into lappets, opening posterior and median; on Decapoda Anomura. *Triangulus* G. Smith, resembles *Lernaeodiscus* in many respects, but mantle opening asymmetrically situated; on Decapoda Anomura. *Sylon* Kröyer, egg-shaped, mantle opening paired, anterior; on Decapoda Macrura. *Clistosaccus* Lilljeborg, irregularly oblong, mantle opening absent; on Decapoda Anomala.

Incertae sedis. *Duplorbis* G. Smith, on the Isopod *Calathura*; *Apeltes* Lilljeborg; *Thompsonia* Kossmann; *Thylacoplethus* Coutière.

Sub-order 5. ASCOTHORACICA.

These are parasitic, hermaphrodite or dioecious Crustacea generally living embedded in the tissues of their hosts. They are perhaps allied to Cirripedes but present no very clear affinities with any of the other sub-orders. A nauplius larva is found in *Laura*, and in *Dendrogaster* a later larval stage is known which somewhat resembles the Cypris larva of the Cirripedes. The antennae are, however, formed on a quite different plan, and no peduncular attachment is found in any of the four genera.

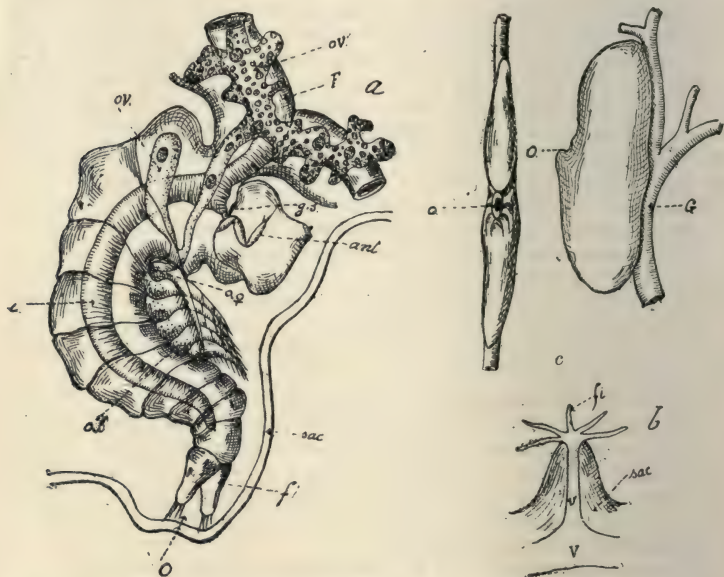


FIG. 279.—*Laura gerardiae* Lacaze-Duthiers. *a*, body partly removed from the sack; *b*, a papilla from the outer surface of the sack; *c*, complete sack attached to the skeletal stem of *Gerardia* (*G*), with the orifice towards the spectator, and in profile. *ant.* antennae; *f* caudal fork; *F* hepatic diverticulum contained between the layers of the mantle sack; *g.s.* supra-oesophageal ganglion; *i* intestine; *o* ♂ (?) male orifice; *o* ♀ female orifice; *O* opening of sack; in *a*, *O* shows the position of the opening; *ov* ovary; *v* vessels. (From Gruvel, after Lacaze-Duthiers.)

The single pair of antennae are short and pointed and the mouth parts are contained in an oral cone. Five or six pairs of appendages, simple or biramous (absent in adult of *Dendrogaster*), succeed and a pointed abdomen may be present, terminating in a caudal fork. Diverticula of the alimentary canal and the ovaries lie between the layers of the mantle.

Laura gerardiae Lacaze-Duthiers (Fig. 279) * lives enveloped, except for a small orifice, by the polyps of the colonial antipatharian *Gerardia*, L.-Duthiers (*Savaglia* Nardo). The enormously developed mantle, or sack, contains between its folds the ovaries (*ov*) and diverticula of the alimentary canal (*F*), and its surface is beset with prominences (*b*) embedded

* H. de Lacaze-Duthiers, Histoire de la *Laura gerardiae*, Mém. de l'Acad. des Sciences, T. 42, Paris, 1882.

in the tissues of the *Gerardia*, from which it appears that *Laura* derives a large part of its nourishment. There are 6 pairs of uniramous thoracic appendages, and a 3-segmented abdomen, ending in a caudal fork (*f*). Mediterranean. *Dendrogaster* * *astericola* Knipowitsch, parasitic in the body cavity of *Echinaster sanguinolentus* and *Solaster endeca*. The greatly developed mantle of the female (of which alone the adult is known) encloses the body except for a small aperture, and is produced laterally into five irregular lobes, which, as in *Laura*, contain the ovaries and diverticula of the stomach. The alimentary canal ends blindly. The mouth parts are reduced, and other appendages are absent in the adult. The larva carries a greatly developed antenna consisting of four short stout joints, without a sucker but bearing a long whip-like olfactory appendage. There are 5 pairs of long setose thoracic appendages (the 1st thoracic being absent, according to Claus) and a long 6-jointed abdomen. White Sea. *Petrarca bathyactidis* Fowler, in the mesenterial chambers of the coral *Bathyactis symmetrica* obtained at a depth of 2,300 fathoms, off Japan. The mantle forms a bivalve shell. The abdomen is rudimentary. Hermaphrodite. *Synagoga mira* Norman,† an external parasite on the surface of the colonies of *Antipathes larix* Ellis, at Naples, with 6 pairs of biramous thoracic appendages and a well-developed caudal fork.

Sub-class 2. MALACOSTRACA.‡

The name Malacostraca was given by Aristotle, as explained above (p. 360), to a group of Crustacea now classed in the Decapoda. §

* N. Knipowitsch., *Beit. z. Kennt. Ascothoracida*. (In Russian, with German abstract.) *Tran. Soc. Nat. Petersbourg*, T. 23 (1892), p. 134.

† *Br. Ass. Rpt.*, 1887, p. 86.

‡ Besides the works of Latreille, Milne Edwards and Dana compare W. E. Leach, *Malacostraca podophthalma Britanniae*, London, 1817-1821. Th. Bell, *A History of the British stalk-eyed Crustacea*, London, 1853. C. Heller, *Die Crustaceen des südlichen Europa*. Wien, 1863. C. Spence Bate and J. O. Westwood, *A History of the British sessile-eyed Crustacea*, vols. I and II, London, 1863-68. G. O. Sars, *Hist. naturelle d. Crustacés d'eau douce de Norvège*, Christiania, 1867. Id. *An account of the Crustacea of Norway*, vol. 1, *Amphipoda*, 1895, vol. 2, *Isopoda*, 1899, vol. 3, *Cumacea*, 1900. Y. Delage, *L'appareil 'circul. des Crustacés Edriophthalmes marins*, *Arch. Zool. exp. et gén.* I. ix, 1881. Faxon, *Selections from Embryological Monographs*, I, Crustacea, *Mem. Mus. Comp. Zool. Harvard Coll.*, Cambridge, Mass., 1882. A. Gerstaecker and A. E. Ortmann, *Crustacea Malacostraca in Bronn's Tierreich*, Leipzig, 1881-1901. J. E. V. Boas, *Vervandtschaftsbez. der Malacostraken*, *Morphol. Jahrb.* Bd. VIII (1883), p. 485. E. Korschelt u. K. Heider, *op. cit.* on p. 342. H. J. Hansen, *Zur Morphologie der Gliedmassen u. Mundtheile bei Crustaceen u. Insecten*, *Zool. Anzeiger*, I, xvi. (1893), pp. 193-198 and 201-212. T. R. R. Stebbing, *Crustacea*, London, 1893. C. Claus, *Neue Beitr. z. Morph. d. Crustaceen*, *Arb. Zool. Inst. Wien.* vi. (1896). W. T. Calman, *On the Classification of the Crustacea Malacostraca*. *A. and M. of N. Hist.* (7), xiii, 1904.

§ For the subdivisions of the Malacostraca here adopted, see the Table of Contents.

Some Malacostraca (e.g. Tanaidacea, Cumacea) are small, but many attain a much larger size than any of the Entomostraca.

In contrast with the varying number of segments in the post-cephalic region of the body met with in the several groups of the Entomostraca, and especially in the Phyllopoda, the Malacostraca possess a constant number. Eight segments are found with great uniformity in the thorax, and seven, including the telson, in the abdomen. These regions are clearly marked by the character of their appendages, and frequently by the difference in the mobility of their segments, those of the abdomen being the most mobile. The only exceptions to uniformity in the number of segments are met with in the Leptostraca (*Nebalia* and its allies) which are in many respects intermediate between the Phyllopods and the Eumalacostraca, and have 8 segments in the abdomen; in some aberrant forms of Amphipoda, whose relation to the main body of the order which conform to rule is undisputed; and in the Decapod *Leucifer*, in which the eighth thoracic segment is not differentiated, and its appendages and those of the seventh segment are absent.

In the stereotyped number of the segments of the regions of the body the Malacostraca may be compared with the Insecta, which occupy a corresponding position at the head of the Antennata. A similar uniformity in the number of segments, which presents great variation in the lower members of a phylum, is found in the cervical region of mammals among Vertebrates.

The head is marked off from the thorax by the character of its appendages, and in the least differentiated Malacostraca—*Nebalia*, (?) *Anaspides* and the Holotrophous Schizopods*—by a groove between it and the first thoracic segment.

A dorsal shield is present in many groups of Malacostraca investing some or all of the segments of the thorax. In *Nebalia* and the Lophogastridae the shield appears to be a purely cephalic structure, a fold of the integument of the dorsal and lateral regions of the head, and the thoracic segments, though covered by it, do not participate in its formation. In the other shield-

* In Sars' figure of *Gnathophausia longispina*, in the *Challenger* Monograph on the Schizopoda (Pl. 8, Fig. 17) the first thoracic segment appears to be limited in front by a definite groove, which would thus separate the cephalic and thoracic regions. If this is the case the dorsal shield in this genus is a purely cephalic structure.

bearing groups, however, the base of the fold has extended backwards and involved the terga of some or all of the segments of the thorax, becoming in them a cephalothoracic shield. To whatever degree the thoracic terga may be involved in the shield its edges always project freely, investing the sides of the thorax more or less closely, and the space thus enclosed may be converted (Cumacea, Chelifera, Decapoda) into a respiratory chamber.

In *Anaspides*, Isopods and Amphipods a dorsal shield is absent, and in the two latter orders the first thoracic segment (in the Laemodipoda the first and second) is completely fused with the head, forming a short cephalothorax.

Behind the last appendage-bearing segment of the abdomen there is in most Malacostraca a simple median plate, the **telson**, with the anus opening on its ventral surface. In some forms (*Astacus*), the telson is incompletely divided by a transverse suture. In the Leptostraca two setose processes, jointed in the larva, project backwards, one on either side of the anus, constituting a caudal fork of the type found in the Phyllopods and Copepods. This structure recurs in the larval stages of the Mysidae, the protozoa stage of *Penaeus*, and in a larva which has been referred to the Stomatopods (p. 509).

Head appendages. Unlike those of the Entomostraca the *first antennae* of the Malacostraca are frequently bi-, sometimes triramous in the adult, though uniramous in the larva. An otocyst is present in the basal joint in *Anaspides* and in most Decapoda. The *second antenna* has a 2- or 3-segmented protopodite, bearing a many-jointed flagellar endopodite, the three basal segments of which are generally enlarged. The exopodite when present usually consists in the adult of an oval or truncated unsegmented scale, frequently fringed with setae. It is absent in Cumacea, Amphipoda and most Isopoda. The antennary (excretory) gland opens (except in Isopoda, where it is wanting) on the ventral aspect of the proximal segment in cases where the protopodite consists of two segments, on the second where it consists of three.

The basal segment of the *mandible* is produced inwards into a prominent masticatory lobe, working against its fellow. The shape of this lobe presents considerable modifications. It may be simple, as in *Astacus*, but it is often produced into two pro-

cesses, an anterior cutting point or blade, and a posterior "molar" surface, separated from the anterior process by a deeper or shallower notch. In the notch a row of movable spines may be present, the anterior of which, larger than the others, was named by Hansen the *lacinia mobilis* (Fig. 280). Curiously enough this accessory blade is, as pointed out by Boas and Hansen, characteristic of the mandibles of those divisions of the Malacostraca, in which the young are developed in brood pouches, and absent in the others (p. 454). The distal segment of the protopodite, together with the endopodite, constitute the 3-jointed mandibular palp, which is only absent in the Cumacea, wood-lice, Attyidae, the



FIG. 280.—The cutting edges of the mandibles, *a* of *Euphausia pellucida* (Euphausiidae), *b* of *Anchialus typicus* (Mysidae), the latter showing the *lacinia mobilis* (l.m.).

zoaea larva and a few other cases.

In the *first maxilla* the first and third segments, according to Hansen,* are produced inwards as setose

cutting blades. The endopodite may be a small lobe in continuation of the axis of the limb, but in the Cumacea, Chelifera and Lophogastridae it is longer and strongly reflexed, and in the Leptostraca it is a long many-jointed flagellum (Fig. 284). A small lobe often projects on the outer surface of the limb, and may represent the exopodite. The segments of the protopodite of the *second maxilla* are produced inwards into two masticatory lobes which may, as in *Astacus*, be subdivided. A 1- or 2-segmented endopodite is frequently present and the exopodite forms a more or less fanlike plate, which in the Decapods, where it is large and known as the *scaphognathite*, regulates the flow of water through the respiratory chamber. Both endopodite and exopodite are reduced or absent in the Cumacea, Isopods and Amphipods. In the parasitic forms of the last two orders the mouth parts are modified in relation to the suctorial habits.

A negative feature of the cephalic appendages is the absence of the branchial epipodite or epipodites frequently found on those of the thorax.

* Not the two basal segments, as usually stated.

Thoracic appendages. In the lower members of the Malacostraca these form a uniform series, the members of which present little or no departure from a common plan.

In *Nebalia* they have the broad foliaceous character, with faintly marked articulations, found in the Phyllopoda. The short, narrow and jointed endopodite approaches the malacostracan type, but the unsegmented exopodite and large flat epipodite, notched on the outer side, are entirely phyllopodan (Figs. 284 and 285).

In *Anaspides* the eumalacostracan thoracic appendage is found in what appears to be, in many respects, a primitive form (Fig. 287 B). The 2-segmented protopodite is prolonged into the stout ambulatory endopodite, and the flagellar exopodite springs from the outer side of its second segment (basipodite). The basal segment (coxopodite) bears on its outer side two simple lamellar gills, the epipodites.

The biramous character of the thoracic legs is preserved throughout the Schizopoda, and in the larval stages of many Decapods. In the majority of the latter it is only retained by the three anterior legs of the adults (maxillipeds) though in some of the Penaeidea and Caridea an exopodite persists throughout life on all the legs. Three to five of the legs in the middle of the thoracic series, in the Cumacea, retain the flagellar exopodites, and they may be present in a reduced form on the second and third thoracic limbs of the Chelifera. The Isopoda and Amphipoda are devoid of thoracic exopodites. In the Stomatopoda they are present on the last three legs.

The *epipodites* present an interesting series of modifications in the Malacostraca. Starting from the pair of simple appendages of *Anaspides* (Fig. 287) we find one of them, little modified except that its attachment is shifted to the posterior or even to the inner aspect of the limb, forming the thoracic gills of the Amphipoda. The other appears, as suggested by Claus, to have undergone a change of function and to be represented in the female by the *oostegite* in those orders of Malacostraca in which the development of the young takes place in a brood pouch.

Oostegites are broad and almost membranous plates, attached to the bases of certain of the limbs, which, overlapping those of the other side, enclose a space beneath the ventral surface of

the thorax in which the eggs are contained and the young develop.*

In the Branchiopoda we have seen that the number of epipodites of the thoracic legs varies from one to three, and there is evidence of a corresponding variability in number in the Malacostraca, though the homology of the epipodial structures in the several orders remains to be elucidated.

In the holotrophic Schizopoda the highly subdivided gill apparently represents one epipodite, the oostegite apparently represents another, and a rudimentary appendage described by Sars in *Gnathophausia* (p. 465) is perhaps a vestige of a third. It is to be noted that though in both Hemitropha and Holotropha the majority of the gills, when present, have assumed a highly complex form, that of the first thoracic leg in the Holotropha retains the simple condition met with in *Anaspides* and the Amphipods.

In the Decapods four separate branchiae may be present in relation with each thoracic limb (Fig. 317). They are inserted (1) on the coxopodite (podobranchiae) and the gill filaments then often spring from the surface of an epipodial plate, (2) on the arthrodial membrane intervening between the coxopodite and the thorax (arthrobranchiae), and (3) from the surface of the thorax above the insertion of the appendage (one or two pleurobranchiae). But, although so attached in the adult the pleurobranchiae are seen to spring in the larva from the bases of the limbs (Claus), and the branchiae are probably all to be regarded as originally epipodial in origin (Fig. 317). The five anterior thoracic legs of the Stomatopoda bear each a simple epipodial lobe on the basal segment.

The condition of the gills of the Laemodipoda (Amphipoda) is remarkable in that some of the thoracic segments have lost all other trace of appendages, but the gills (epipodia) remain, attached to their ventral surfaces.

The uniformity which exists throughout the series of the thoracic legs in the lower Malacostraca is modified in varying degrees in the more differentiated groups by the adaptation of one or more of the anterior members as *maxillipeds*, to subserve,

* There are, however, among the Isopoda, instances of the formation of a ventral brood pouch by structures, the relation of which to epipodial oostegites appears remote and has not been made out.

together with the jaws proper, the prehension and mastication of the food.

The first thoracic leg is thus modified in *Anaspides* by the development of jaw-like endites on the coxopodite (Fig. 287 A), in the Holotropha by the shortening of the limb, and in the Isopoda and Amphipoda by the shortening and more or less complete fusion of the pair of limbs to form a labium-like lower lip (Figs. 296 and 306). In the Cumacea and Decapoda three pairs of thoracic legs are modified as maxillipeds and in the Stomatopoda five pairs may be so regarded (Fig. 309). When more than one pair of maxillipeds exist the anterior are generally the most jaw-like, the posterior being transitional in character to the limbs behind them.

The coxopodites of the thoracic legs of the Isopoda and Amphipoda may be expanded and so closely united with the thoracic segments that bear them as to be immovable, and the joint between the coxopodite and basipodite acquires a corresponding increase in mobility.* In some cases all trace of their separation from the body segment is lost.

Of the **abdominal appendages** the five anterior pairs (*pleopoda*) are often the main agents in gentle swimming movements, while the terminal pair, the *uropods* form with the telson the powerful fanlike tail-fin of several groups of Malacostraca. The abdominal appendages are biramous limbs in which the two branches spring from a frequently 2-segmented protopodite. Their various modifications are described under the several orders, but it may here be mentioned that they sometimes bear the chief respiratory organs of the body, either (Isopoda) by the transformation of the endopodites alone, or of both rami into lamellar gills, or (the Isopod *Bathynomus*) by the growth of long respiratory filaments fringing the endopodite, or (Stomatopoda) by the development of a peculiar complex gill on the exopodite. The presence of tubular air-passages in the exopodites of two or more of the anterior abdominal limbs of some wood-lice (Fig. 302) is of interest by analogy with the tracheae of *Peripatus*, some Arachnids, the Antennata and the Siphonophoran *Velella*. A process from the base of the inner margin of the endopodites of the pleopods is present in Leptostraca, Hemitropha

* See footnote p. 495.

and many Decapods. It is known as the *appendix interna* or *stylambilis* (Fig. 319). In many cases, at least, it carries hooks, and serves, with its fellow, to couple the pair of limbs together.

The presence of a masticatory **stomach** has already been alluded to as a feature of the Malacostraca (p. 351). The Stomatopods are remarkable in the disposition of the hepatic glands, consisting of caeca segmentally arranged along ducts which open anteriorly into the stomach (Orlandi). A somewhat similar arrangement is found in the Pagurid *Coenobita*.*

The position of the **genital apertures** in relation to the segments is, so far as it has been ascertained, constant and characteristic: that of the oviduct on the sixth, that of the vas deferens on the eighth thoracic segment. In either case the position of the apertures may be on the sternite of the segment, or (some Decapoda) on the coxopodites of the limbs, or on the arthrodial membranes at the bases of the limbs.

The **segmental glands** of the second antennae often act as excretory organs in adult Malacostraca, although those of the second maxillary segment replace them in Stomatopods, the Chelifera, some Isopods and the Cumacea. In *Nebalia* the glands of both segments coexist in the adult.

The **central nervous system** of the Leptostraca and of *Apseudes* (Chelifera) (Fig. 241) approaches very closely to the condition found in the Phyllopoda. The ganglia of the second antennary segment have joined the brain, of which they form the posterior lobes, but a transverse commissure passing between the two longitudinal bands of the oesophageal ring and behind the oesophagus apparently contains the commissural fibres which unite them with one another, and thus by its position records their original postoral situation. Each pair of appendages behind the second antennae is represented by a distinct pair of ganglia, and double longitudinal commissures run throughout the series. In the larva of *Nebalia* a seventh abdominal ganglion is present (corresponding to the seventh abdominal segment), behind that of the last limb-bearing segment. In some members of the higher groups, as *Sphaeroma* (Isopoda) and *Euphausia* (Schizopoda), the nervous system is in an almost equally simple

* Cf. Borradaile, in Gardiner's *Fauna and Geography of the Maldives and Laccadives*, Vol. i., p. 80.

condition, but on the whole, as the segments of the body become approximated together and lose their external distinctness (and the approximation is doubtless accompanied by an increase in the complexity in the co-ordinating mechanisms by which the movements of their appendages are bound together) so do their corresponding neuromeres merge one with another. The concentration is complete in the Brachyura, where, in such forms as the Spider Crabs (*Maia*, Fig. 241, *F*) the ganglia of all the postoral segments are fused into a common star-shaped mass in the thorax, from which the nerves radiate to the several parts of the body.

A number of species of Malacostraca with thin and transparent cuticle are capable of changing their colour, in varying degrees, in relation to their surroundings. The phenomenon was investigated by Pouchet,* and more recently, in two remarkable papers by Keeble and Gamble.† Only some of the results can be touched on here.

The *chromatophores*, in which the pigment is lodged, are in the Decapods multinuclear bodies, probably clusters of cells, together forming a central mass, with branching processes, which anastomose with those of neighbouring chromatophores. Each chromatophore may contain a number of pigments of different colours. Some (reds and yellows) are light-transmitting pigments, others (white, yellow and blue) yield their colour when seen by reflected light. The pigment expands and contracts within the chromatophore, without alteration in shape of the latter (as has also been shown to be the case in the frog). There is reason to believe that each separate pigment is contained in a separate cell or group of cells.‡

The chromatophores of Decapods are classed in two systems. (1) The *primary system* is deep-lying and mainly in relation with the ganglionic centres (segmental and visceral). It is developed in the larva and closely resembles that of the adult Schizopod *Macromysis*; (2) a *secondary system*, more super-

* G. Pouchet, "Les changements de Coloration sous l'influence des nerfs," *Journal de l'Anat. et de la Physiologie*, T, 12 (1876).

† *Hippolyte varians*, a study in Colour-change, *Q.J.M.S.*, vol. 43 (1900), p. 589, and the Colour-Physiology of higher Crustacea, *Phil. Trans. B.* vol. 196 (1904), p. 295.

‡ In addition to pigment *Hippolyte* has in its chromatophores a mobile colourless fat which expands and contracts with the pigments.

ficial in position, and in the adult Decapod completely masking the primary; though this, none the less, persists.

When the chromatophore pigment is expanded, a network of colour, close or open, pervades the body, either continuously or in certain parts, and then forming a pattern which in most species is constant and characteristic. When it is contracted the pigment forms an inconspicuous dot in the chromatophore, and the body of the Crustacean becomes transparent and apparently colourless, though in some cases a diffused blue colour remains.

The movements of the pigment occur in response to light, the action being direct and indirect. (1) The direct action of the light is to cause expansion of the pigment. In the dark it contracts and the degree of expansion varies with the intensity of the illumination. (2) The indirect action of light is effected by the nervous system through the mediation of the eyes. The response is not to the intensity of the illumination, but to the colour of the background against which the prawn finds itself. A dark background causes expansion of the pigment, in *Macro-mysis*, *Palaemon* and *Hippolyte*, even though the light be dim; a light background causes contraction. At night (absence of direct stimulus of light) the pigments contract, the animals becoming transparent. The colour pattern develops again at dawn.

An astonishing variety of colour coats is at the disposal of *Hippolyte varians*, enabling the individuals of this species to blend in colour with their surroundings. They are of very sedentary habit and only quit hold of the weed among which they live when it is roughly shaken. They may be found of uniform brown, red, pink, grey or emerald green colour, or broad bands or blotches or thin lines of these colours may traverse the otherwise transparent body. The pattern, uniform or localized, is found to correspond with the degree of subdivision of stems or branches of the weed which the prawns inhabit. When removed from their natural habitat and given a choice of weed they take refuge in that which they most closely resemble. By prolonged residence (some days) among weed of a different colour, the colour of the coat pattern of the prawn may vary in correspondence—e.g., brown becoming green or vice versâ.

Although the colour is thus adaptable to that of the environ-

ment, the day pattern of the adult prawn does not vary in distribution. But in the adolescent stage a permanent change in the pattern of individuals with a coat of lines or bars may be induced by appropriately altering their surroundings, leading them to assume, e.g. a uniform coat by extension of the superficial pigment-tracts over the body, and this becomes the permanent adult coat. In this result the character of the stimulus received by the eye is an essential factor in the change, i.e., in the resulting increase in the number of the chromatophores.

When *Hippolyte varians* is against a dark background, there is, as stated above, an alternate expansion and contraction of the pigment of the chromatophores in response to day and night. If these prawns are left in the dark, Keeble and Gamble have found that, for some 70–80 hours, an expansion of pigment occurs during the recurring diurnal periods though gradually lessening in intensity. Thus the rhythmic expansion and contraction of the pigment set up in response to alternating day and night persists after the conditions of illumination have been rendered uniformly nocturnal.

The conclusion as to the effect of background in modifying the distribution of the pigment in the Crustacea presents a parallel with some of Poulton's results on the development of colour in the larvae and pupae of Insects.* For a fuller statement of the highly interesting and suggestive results obtained, the reader is referred to the original memoirs.

Modification of the reproductive system produced by parasites.—Giard has drawn attention to the remarkable effects produced by parasites on the organization of their hosts, both animal and vegetable. Conspicuous instances are furnished by the malacostracan Crustacea, in which group further evidence has been brought to light by the work of Geoffrey Smith.† The parasites producing this result belong to several species of the cirripede Rhizocephala, the internally parasitic Isopod Entoniscidae, and the allied externally parasitic Bopyridae. The effect on the general metabolism varies in different groups. In the case of the Brachyura affected by Rhizocephala, ecdysis ceases from the moult at which the parasite becomes external

* E. B. Poulton, *Phil. Trans.* vol. 178, B. (1887), p. 311.

† Rhizocephala. *Fauna and Flora des Golfes von Neapel*. Monog. (29), 1906.

until its death. In the Hermit Crab, *Eupagurus*, on the other hand, ecdysis is continued, and growth may even (as in capons) be accelerated by the presence of the parasite. The effects of the parasitism, on the hosts, are manifold. In the first place it leads to a more or less complete atrophy of the gonads, out of all proportion to the effects on the other organs of the body.

A further effect is apparent in the modification of the secondary sexual characters of the host. In the case of the female hosts these characters may undergo reduction. Thus in the females of a Crab, *Inachus*, affected by *Sacculina*, the swimmerets which appear at the last moult, and especially their ovigerous endopodites, are reduced in size. In the males, not only are the secondary male characters, the copulatory styles (first abdominal appendages) and chelae, reduced in size, but there is a definite assumption of female characters in addition (Fig. 281). Thus it has been found that there is a tendency for the infested males to become hermaphrodite. In *Inachus* the abdomen becomes longer and broader, the posterior abdominal swimmerets (3-5), which have disappeared since the later larval (Megalopa) stages, grow again, and even, in some cases in which the gonad is not completely aborted, it is found to develop ova as well as spermatozoa, although, owing to the occlusion of the ducts, the products can never be shed.

Results similar to those in *Inachus* have been obtained by Smith in *Pachygrapsus*, and Potts has found that *Eupagurus meticulosus*, infested by *Peltogaster*, exhibits similar effects though in a more pronounced degree. Potts concludes that in this species ova are developed in the gonads of all infected males, after the parasite has become external. For further details on these striking results the reader is referred to the original memoirs.*

Development.—The eggs of some groups of the Malacostraca pass through their development in the brood space of the mother, being contained either between the thoracic legs and protected by the lobes of the shell (Leptostraca) or between the oostegites and the ventral wall of the thorax, as in the Cumacea, Isopoda, Amphipoda, Chelifera, and the Schizopod families, Lopho-

* See too the recent botanical work by Strasburger, *Versuche mit diöcischen Pflanzen in Rücksicht auf Geschlechtsverteilung*, *Biol. Centralblatt*, T. xx (1900), p. 689.

gastridae and Mysidae.* The young, in these cases, leave the brood pouch in a form identical, or nearly so, with that of the

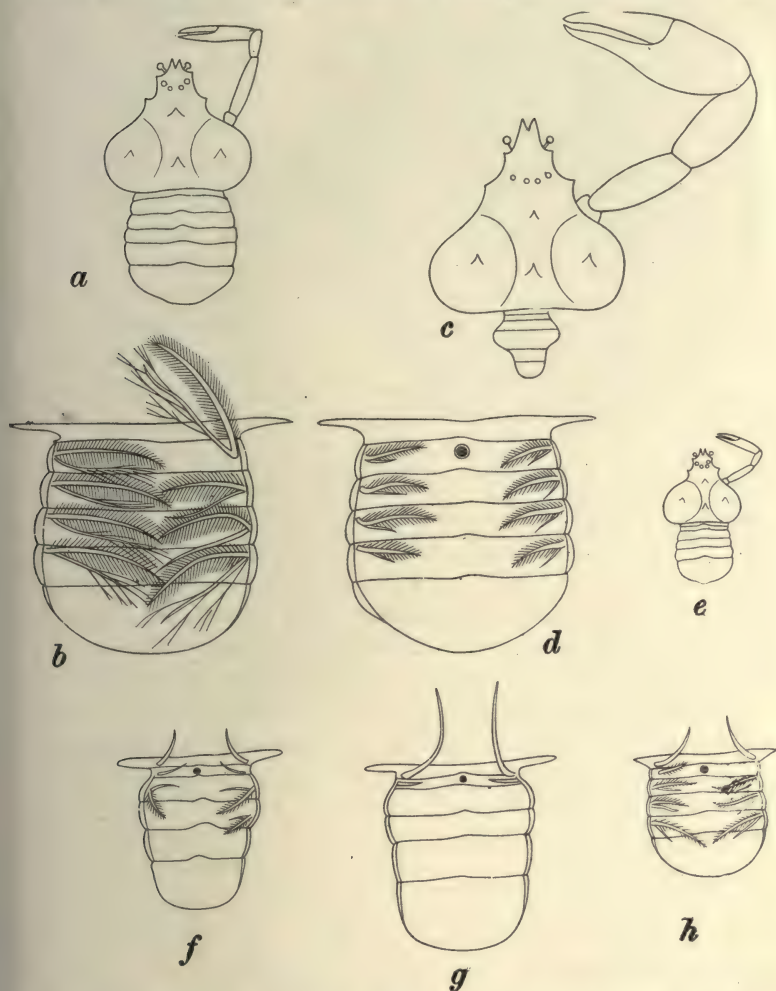


FIG. 281.—The effects of parasitism on *Inachus*. *a* normal adult female, natural size; *b* ventral view of abdomen $\times 2$; *c* normal "high" male, natural size; *d* ventral view of adult infected female $\times 2$; *e* infected male, modified into hermaphrodite form, natural size; *f*, *g*, *h* abdomina of infected males $\times 2$, showing degrees of approximation to the female condition (*h* the abdomen of the specimen *e*) (after G. Smith).

parent, although in several groups (Leptostraca, Mysidae,

* These Malacostraca are united by Calman in the group Peracarida, cf. p. 453 et. seq.

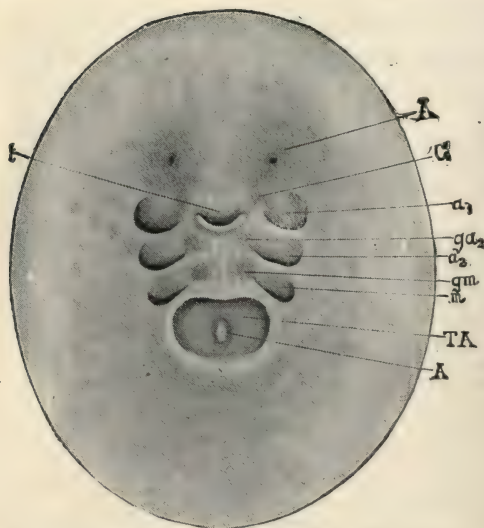


FIG. 282.—Embryo of *Astacus fluviatilis* in the nauplius stage. *A* (above) rudiment of eye; *a'*, *a''* first and second antenna; *G* cerebral ganglion; *G2* ganglion of the second antenna; *gm* ganglion of the mandible; *l* upper lip; *m* mandible; *TA* thoraco-abdominal rudiment; *A* (lying in *TA*) anus (from Lang, after Reichenbach).

Isopoda) a well-marked stage with two pairs of antennae and mandibles, followed by the shedding of a larval cuticle, has been recognized in the development of the egg as corresponding to the nauplius larva of other Crustacea. (Compare the corresponding stage in the development of the fresh-water crayfish, Fig. 282.)

In the remaining Malacostraca, i.e., in the Euphausiid

Schizopods, in Stomatopods and Decapods (for the development of the Syncarida see p. 462) a metamorphosis presenting varying degrees of completeness is nearly always found in the life-history.

Compared with the gradual series of stages which in the Phyllopod Branchiopods and most Copepods leads from the nauplius larva to the adult condition, the metamorphosis of the Malacostraca is characterized by somewhat abrupt transitions from one larval stage to another, and by the introduction of stages which are not in the direct line leading to the adult form. "The metamorphosis of the lower Crustacea thus bears the same relationship to that of

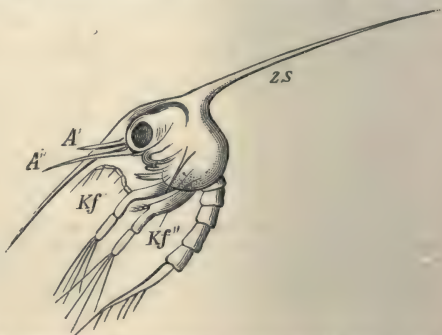


FIG. 283.—Crab zoea (*Thia*), after the first moult. *A'*, *A''* first and second antennae; *Kf'*, *Kf''*, the two pairs of biramous appendages corresponding to the first and second pairs of maxillipeds; *ZS* zoea spine on the back (from Claus).

the Malacostraca as does incomplete to complete metamorphosis among Insecta" (Korschelt and Heider).

Prominent among these intercalated larval forms is the *zoaea larva* in which (Fig. 283) the appendages of the head and of the first and second (in some cases the third in addition) thoracic segments are well developed, and the abdomen distinctly segmented, while the posterior thoracic segments are barely differentiated and their appendages absent. The larva swims by means of the exopodites of the maxillipeds, and by the abdomen, and the cephalothoracic shield is generally produced into long spines, which limit its motion in certain directions. It is also characterized by the absence of the mandibular palp. A *zoaea larva* of this type occurs very generally among the Decapoda, and in the Euphausiidae (Fig. 291), and in a somewhat different form in the Stomatopoda (Fig. 312, p. 510).

The stage at which free larval life is begun varies much in the several groups, and, apart from the orders mentioned above in which the eggs are contained in a brood space, it is generally retarded most in the more differentiated members of the series. It may also be retarded in species living in fresh-water or on land—a feature in which, as Fritz Müller pointed out, the Crustacea agree with other groups of animals.*

In *Euphausia* (Thysanopodidae, Fig. 291) and *Penaeus* (Fig. 323) (Decapoda) the life-history begins, as in many Entomostraca, with the *nauplius* stage, in *Leucifer* (Decapoda, Fig. 324) and perhaps also in some Stomatopoda (see p. 508, Fig. 310, a), with the *metanauplius*, in which, in addition to the limbs of the nauplius, rudiments of the two pairs of maxillae and of the first (and sometimes also the second) maxilliped, have appeared, and the abdomen ends in a caudal fork.

Sergestes, among the Penaeidea, hatches in the *protozoaea* stage, with the limbs which are rudimentary in the meta-

* *Facts for Darwin*, p. 47, London, John Murray, 1869. In this connexion the case of *Palaemonetes varians* is of interest. The young of the variety living in the sea, on the shores of Northern Europe (but also in brackish or fresh water) are hatched as Zoeae, in which the abdominal legs are still absent, while the exclusively fresh-water forms of the S. of Europe hatch in a more advanced stage, in which these legs are present as biramous buds. (Cf. P. Mayer, *Carcinologische Mitth.* 9. Die metamorphosen v. *P. varians*, *Mitth. Zool. stat. Neapel*, Bd. ii, 1881. J. E. V. Boas, *Kleinere carinol. Mitth.*, *Zool. Jahrb. Syst.*, Bd. iv, 1889.) Some fresh-water Caridea, however, show a contrast with their marine relatives in the opposite direction, having a less abbreviated larval development.

nauplius stage of its allies fully developed, but with the abdomen still incompletely segmented. The paired eyes have here begun to appear, as lateral outgrowths of the head.

The *zoaea*, already described, ushers in the life-history of most Caridea, the Anomura and most Brachyura.

The *Mysis* stage (which would perhaps be more correctly called the Euphausia stage, cf. p. 454) is the initial phase of the marine Macrura Reptantia (Fig. 327), and follows the *zoaea* stage in the Thalassinidea among the Anomura. The full equipment of thoracic legs is attained, and they bear flagellar exopodites. The abdominal limbs develop during this stage.

The remarkable pelagic *Phyllosoma* larva ("Glass Crab") of the Loricata must be regarded as a highly modified form of the mysis stage (Fig. 326). In contrast with the heavily built adult forms the larvae are delicate, glassy, leaf-like organisms expanded in a horizontal plane, with a narrow constriction between head and thorax, a rudimentary abdomen in the earlier stages, and long, very slender biramous thoracic legs.

The fresh-water Macrura Reptantia (the Potamobiinae and Parastacinae) are hatched almost in the adult condition, though the young of the former—the crayfishes of the N. Hemisphere—pass through a stage in which they are said to resemble the latter—the crayfishes of the S. Hemisphere.

The mysis stage does not appear in the life history of the remaining Anomura, or of the Brachyura, in which the transition to the adult condition occurs direct (in the latter with intermediate metazoea and megalopa stages, Fig. 330) from the *zoaea*.

In the following table the groups of the Decapod Crustacea are arranged so that we pass, on the whole, from generalized to specialized forms, and the main larval stages are, in each case, indicated by dashes.* The specialization is indicated, among other features, by differentiation in the series of thoracic appendages, reduction of the trunk limbs (see p. 522) from a biramous to a uniramous type, the differentiation of a branchial chamber beneath the branchiostegite, the coalescence of the neuromeres

* With regard to the Nephropsidae and Scyllaridae, it is not intended to imply that both or either of these families is directly intermediate between the Caridea and Anomura. They stand here as representatives of the type of the Macrurous Reptantia from which it seems probable that the Anomura are derived.

of the ganglionic chain, and in the later members of the series by reduction of the abdomen as an organ of locomotion.

	Nau- plius Stage.	Meta- nauplius Stage.	Proto- zoaea Stage.	Zoea Stage.	Mysis Stage.	Meta- zoaea Stage.	Me- galopa Stage.	Adult Stage.
Penaeidea—								
<i>Penaeus</i> . . .	—	—	—	—	—			—
<i>Leucifer</i> . . .	—	—	—	—	—			—
<i>Sergestes</i> . . .			—	—	—			—
Caridea—								
<i>Hippolyte</i> . . .				— ¹	—			—
Nephropsidae								
<i>Homarus</i> . . .					—			—
Scyllaridae								
(Loricata);								
<i>Palinurus</i> . . .					— ²			—
Anomura . . .								
<i>Gebia</i> . . .				— ³	—			—
<i>Eupagurus</i> . . .				— ⁴		— ⁵		—
Brachyura—								
<i>Thia</i> , etc. . .				—		—	—	—

¹ The Caridid zoea is somewhat more advanced than the typical form, having three pairs of maxillipeds, and a fan-shaped telson, replacing a caudal fork. In *Palaemon*, *Crangon*, and *Palaemonetes vulgaris* rudiments of the 4th and 5th (in the *Palaemon* of the 6th) thoracic limbs are also present.

² The mysis stage in its highly modified Phyllosoma form.

³ With rudiments of thoracic limbs 3-7.

⁴ The 3rd maxillipeds rudimentary.

⁵ The trunk and abdominal limbs are present, but uniramous.

In *Penaeus* the young hatch out as nauplius larvae, but in the great majority of the Decapods, although a well marked nauplius stage, followed by the shedding of a larval cuticle, is passed through in the egg (cf. Fig. 282), larval life begins at a later stage. As will be evident from inspection of the table, the stage at which the larva is hatched becomes, on the whole, more and more advanced, the higher the degree of differentiation of the adult form. In other words there is a tendency to the suppression of the earlier stages of the life-history, as later stages are added. The mysis larva is at the end of the metamorphosis of *Penaeus*, while it initiates that of the lobster.

The occurrence of the mysis stage in the development of many groups of Decapods in which the larva resembles, in several particulars, the least differentiated members of the series, and still more the Schizopods—with one group of which, the Euphausiidae, the Penaeidea are closely allied—is a pheno-

menon which finds many parallels elsewhere. It appears to be comparable with the occurrence of the tailed larva of the Ascidians, of the pharyngeal clefts in the throat of the chick, of the chilarian segment in the embryonic scorpion. In these early stages of the life-history the larva or embryo appears to be dominated by the factors which, in earlier ages, shaped its adult ancestors. When we turn, however, from the mysis to other and still more prevalent larval stages of the Malacostraca, the zoea and the nauplius, such an explanation appears to be only very partially if at all applicable to them. The zoea larva occurs in one form or other, as we have seen, in three groups of the Malacostraca, and persists in the higher Decapods, notably in the crabs, in which the mysis stage is absent, or, as we say, has been obliterated. The nauplius larva occurs either as a free stage, or as a transient embryonic phase, apparently throughout the Crustacea. Yet we have no evidence of the existence, in recent or fossil forms, of a group of Malacostraca in which the posterior thoracic segments were suppressed in the adult state, as they are in the zoea, and the evidence at our disposal as to the ancestral stage of the Crustacea points, as we have seen, not to the three-limbed nauplius, but to a multi-segmented form of the annelidan type. The explanation which is usually offered for the divergence of these larval forms from a phylogenetic type is that they have become adapted to some special conditions of larval existence, and the parallel is drawn, as we have seen, with stages of the complete metamorphosis of the Insecta. Some crustacean larvae, it is supposed, remain dominated by the influence of heredity, while others have struck out new lines in response, now to one set of factors in their environment, now to another.

Without denying the possibility of an explanation on such lines, we may point out that it must be regarded as speculative until the conditions of environment have been recognized to which the very diverse characters of the larvae are adapted.*

* That the physical conditions of the mysis and the zoea larvae need not be very different is apparent from a passage (p. 362) from Mr. S. I. Smith's account of the Early Stages of the American Lobster, *Trans. of the Connecticut Academy of Arts and Sciences*, vol. ii (1873), p. 351: "The larvae (in the first Mysis stage) . . . were seen swimming rapidly about at the surface of the water among great numbers of zoea, megalops and copepods."

It may be replied that we are no further from an explanation of the characters of these larvae than we are from an explanation of the characters of the species and genera of many other living things; and this is doubtless true, but in offering the phylogenetic explanation of the mysis larva the endeavour is made to discriminate among the possible factors from which its characters result, and in doing so it seems well to point out the difficulties with which the problem is beset.

Whatever view we may take of the full significance of the nauplius and zoaea larvae, it appears that the nauplius, from its prevalence throughout the Crustacea, was established as a larval form at a period of development prior to the divergence of the existing groups, and the zoaea at an early stage in the history of the Malacostraca.

In certain respects the nauplius must be regarded as presenting primitive features of the crustacean stock, and especially in the paroral position of the second antennae, the presence of a masticatory endite at the base of this appendage, and the large biramous palp of the mandible. That the segment bearing the second antennae was originally postoral is indicated in the development of many groups of the Arthropoda. This was apparently the adult condition in the Trilobites, and the nauplius retains this as a character of a free-living stage (cf. p. 356). The biramous character of the mandible persists in some Copepods (p. 396), and Ostracods (p. 384). The median eye and the frontal sense organs are also probably to be regarded as primitive features of the nauplius stage.

Of late years the unity of the group Schizopoda has been challenged by Boas and Hansen, and the reasons for its partition have recently been strongly urged by Calman.* It is pointed out that the characters which the two tribes of Schizopods possess in common, and which distinguish them from the Decapods are few in number, and of doubtful value. The modification of the three anterior pairs of thoracic appendages as maxillipeds distinguishes the great majority of the Decapods, but among the Penaeidae it is little marked, and it is hard to draw a dis-

* W. T. Calman, On the Classification of the Crustacea Malacostraca, *Ann. and Mag. of N. H.*, ser. 7, vol. xiii (1906), p. 144.

inction in this respect between the Decapod *Sergestes* and the Schizopod *Gnathophausia*. Great variation in the degree of fusion of the thoracic segments to form a cephalo-thorax is found in Schizopods, and, as Calman points out, the fusion is as complete in *Euphausia* as in any Decapod.

Biramous thoracic legs are widely found among the Malacostraca, and in the lower Decapods as elsewhere. The presence of a single series of subdivided branchiae in the Schizopods, against a possible four to each thoracic appendage in the Decapoda appears a more substantial character, but it is doubtful whether the arthrodial branchiae of the Lophogastridae are precisely homologous with the podobranchial appendages of the Hemitropha.

On the other hand it has been pointed out that though the Schizopoda agree in a general "caridoid facies" their two divisions, Hemitropha (Euphausiidae) and Holotropha (Mysidae and Lophogastridae) are strongly contrasted in many of the characters in which the Decapoda are distinguished from other divisions of the Malacostraca. Thus the Hemitropha agree with Decapods in the absence of a brood-pouch, and, in association with this feature, in the presence of free larval stages in the development; in the participation of all segments of the thorax in the formation of the cephalothoracic shield; in the short capsular heart; the absence in the adult of a lacinia mobilis on the mandible (*see* p. 438) (though there are indications of it in some larval stages) and in the spherical or vesicular shape of the spermatozoa.

The Holotropha, on the other hand, agree with the Cumacea, Chelifera, Isopods and Amphipods in the possession of a brood pouch, in which the young are developed until the full number of appendages is attained. The terga of only the most anterior (or none? Lophogastridae), of the thoracic segments are involved in the dorsal shield, the heart is elongated, a lacinia mobilis is present, and the spermatozoa, so far as they have been observed, are filiform. The two groups also appear to be contrasted in the number of segments of the thoracic limbs, the point at which the main flexure of the limb occurs and in the possession by the limb of a terminal claw.

In reviewing these differences, to several of which attention has been called by Boas and Hansen, Calman has proposed the

name Peracarida * for a group containing all Eumalacostraca possessing a brood pouch, and in this the Holotropha are included, while the Hemitropha are united with the Decapoda in the group of the "Eucarida." The division, Schizopoda, would, on this arrangement, cease to exist.

While admitting that there is much to be said in favour of the course proposed, it appears preferable, in the present work, to retain the group Schizopoda. Zoologists are far from being agreed on the change, and it was strongly resisted by Claus.† Were it adopted the relations of several of the groups of the Malacostraca would still remain highly debatable, and especially that of *Anaspides* to the others.

The Malacostraca fall into two divisions, the Leptostraca and the Eumalacostraca. A tabular view of the divisions of the Malacostraca will be found in the Table of Contents.

Division 1 (and Order). LEPTOSTRACA.‡

Crustacea with a bivalve shell covering the head and middle portion of the body, and a movable head-plate attached in front: with eight well-defined thoracic segments bearing appendages similar to one another, and eight abdominal segments, of which the anterior six bear appendages. The terminal segment carries a caudal fork.

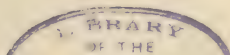
The Leptostraca are small shrimp-like creatures, living in the sea in different parts of the world, from shallow water down to depths of over 2,000 fathoms.

Among the various groups of Crustacea now living the genus

* πῆρα a pouch.

† A piece of evidence against the breaking up of the Schizopoda is contained in the work by Keeble and Gamble, above cited, who find that the colour pattern which is permanent in the holotrophic *Macromysis* is the larval pattern of shrimps. It is, of course, possible that this is a widely distributed pattern in the lower Malacostraca, but in the present state of our knowledge the fact favours the retention of the group Schizopoda.

‡ Besides the works of Leach, Latreille and M. Edwards, compare Claus, *Crustaceensystem*, l.c. Wien, 1876. A. S. Packard, *The Order Phyllocarida and its systematic position. A monograph of the Phyllopod Crustacea, etc.*, Boston, 1883. G. O. Sars, Report on the Phyllocarida, *Challenger Reports*, 56, vol. xix, 1887. Claus, Ueber den Organismus der Nebaliden und die systematische Stellung der Leptostraken, *Arbeiten aus dem Zool. Inst. d. Univ. Wien*, Tom. viii, 1888. J. Thiele, Die Leptostraken Wiss. Ergeb. d. Deutsch. Tiefsee Exped. (Valdivia), Bd. viii. Liefn. 1, 1904. Über die Leptostraken der deutschen Südpolar-expedition, 1901-3. *Deutsch. Südpolar-expedition*, Bd. ix, Heft. 1, Berlin, 1905.



Nebalia and its allies possess a peculiar interest in that while they are not closely related to any, they unite in a remarkable manner the characteristic features of several widely separated

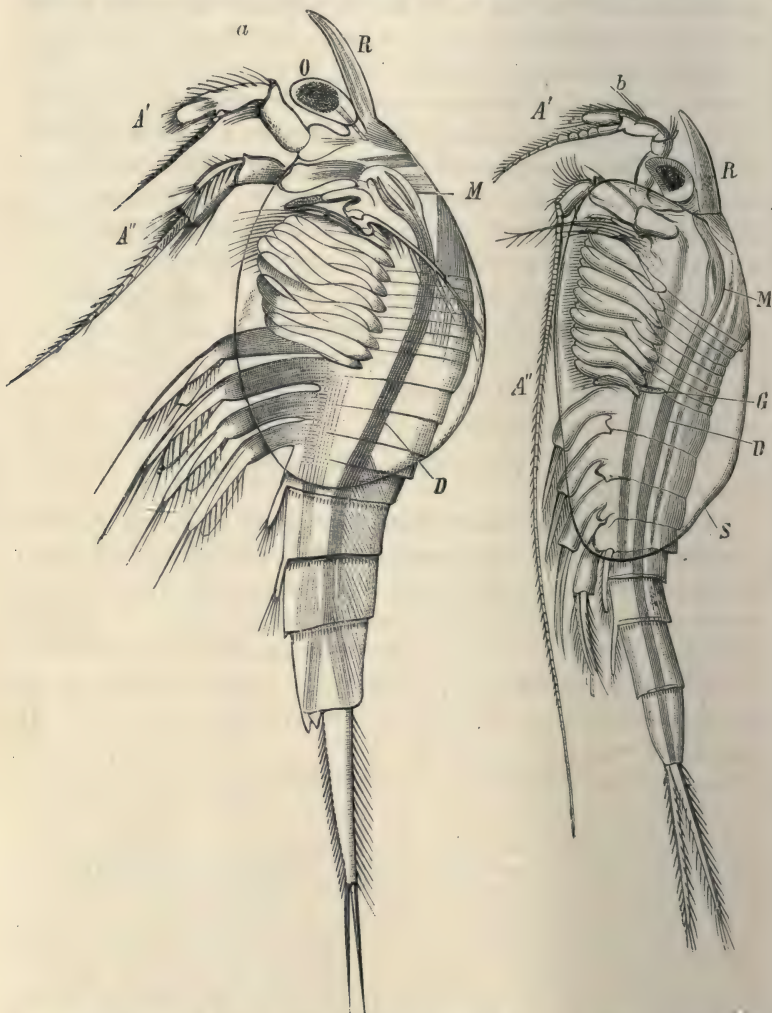


FIG. 284.—*Nebalia Geoffroyi*, strongly magnified (after Claus). *a* female; *b* male; *D* intestine; *G* vas deferens; *M* crop; *O* stalked eye; *R* movable head plate; *S* shell. The flagellum of the first maxilla is directed dorsally in *a*, ventrally in *b*.

orders. They thus appear to represent in a little modified form the crustacean stock in a primitive stage.

The number and arrangement of the limbs is that characteristic

of the Malacostraca. Moreover, in the male, the vas deferens opens at the base of the last thoracic appendages, and the oviduct, in the female, apparently on the sixth. These characters establish the fact that whatever affinities the Leptostraca present to other groups, they are not far removed from the Eumalacostraca.

On the other hand the body is laterally compressed and covered in front by a large bilobed transparent shield, a reduplication of the integument of the head. The two halves of the shield are connected with one another by a **shell muscle**, as in the Cirripedes, Ostracods and bivalved Branchiopods. A pointed **head plate** projects in front of the shield, and presents the unusual feature of being movably articulated with it (Fig. 284, *R*), a character found in palaeozoic Ceratiocaridae, and appearing in a somewhat different form in the Stomatopods. The abdomen is formed of eight segments, including the telson, and is further peculiar in being more or less distinctly differentiated into two regions by the character of its appendages.

The shallow-water forms of the Leptostraca have large stalked eyes (though they are apparently blind in *Nebaliella* (q. v.)), but a median eye is not found. The anterior *antennae* consist of a four-jointed basal region, of which the fourth segment carries an oval setose plate as well as an articulated flagellum. The posterior antennae have three large basal joints and terminate in an articulated flagellum which in the fully grown male is as long as the body and beset with sensory hairs. The cutting *mandibles* bear long 3-jointed uniramous palps. The first maxillae bear two setose plates directed inwards and a long slender dorsally directed terminal flagellum. The second maxilla bears three inwardly directed setose lobes on its inner margin and ends in two short rami.

The fusion between the anterior thoracic segments and the head, which occurs to a greater or less extent in nearly all the Malacostraca, is not found in the Leptostraca. The eight short thoracic segments bear eight pairs of uniform appendages which present a remarkable resemblance to those of Phyllopods (Fig. 285). An obscurely two-jointed basal portion, bearing on its outer surface a two-lobed branchial epipodite (absent in *Nebaliella*) terminates in a jointed and setose endopodite, and in

an exopodite which, in *Paranebalia*, is narrow and setose, and may show some indication of jointing; but in *Nebalia* is expanded into an oval respiratory plate. In the genus, *Nebaliopsis*, the whole appendage is reduced to a short unjointed lobed plate.

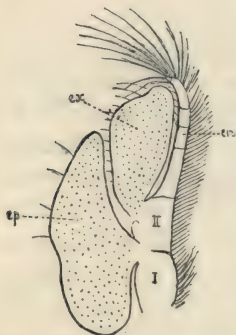


FIG. 285.—A thoracic appendage of *Nebalia*; I and II segments of the protopodite; *en* endopodite; *ep* epipodite; *ex* exopodite (from Lang after Claus).

The anterior region of the abdomen consists of four segments bearing strong swimming feet, having a two-jointed basal portion, and two terminal rami beset with setae. The exopodite is not articulated, but the endopodite has a long distal and a short basal segment, carrying an appendix interna beset with hooks (*retinaculum*) which, with its fellow of the other side, serves to couple the appendages together. The posterior region also consists of four segments, of which the two anterior (three in the larva) bear small unbranched vestigial appendages. The anus opens terminally between two setose appendages, which constitute a caudal fork, like that of *Branchipus*.

The **central nervous system** consists of a large brain and a ventral chain of 17 pairs of ganglia, one for each pair of appendages, from the mandibles to the last abdominal (the two posterior abdominal segments have neuromeres in the larva). The ganglia of each pair lie close to one another, and the cephalic and thoracic ganglia are also approximated longitudinally, while the abdominal part of the chain is more elongated, an arrangement similar to that met with in the Schizopods.

The mouth is guarded by upper and lower lips. Two chitinous masticatory ridges are found on either side of the anterior part of the **stomach** (malacostracan character), and into the posterior part open on the dorsal side two short blind hepatic tubes which project forward over the brain (cf. Cladocera). On the ventral side three pairs of long hepatic tubes open by two common openings. The latter are similar in structure to the hepatic tubes of Isopods and Amphipods. On the dorsal surface of the intestine in the last abdominal segment, lies a short median tube directed backwards and lined by high cylindrical epithelium.

The **excretory organs** are represented by a small antennary

gland in the basal joint of the second antenna, but also by a much reduced shell gland connected with the second maxilla.

The tubular **heart** extends through the thorax and part of the abdomen ; it possesses four large and three small pairs of ostia.

The **testes** and **ovaries** are long tubular structures lying parallel to the intestine. The vas deferens opens on the coxal joint of the last thoracic appendage, and the oviduct was believed by Claus to open on the sixth thoracic segment.

The males differ from the females by their more slender form, the more abundant sensory hairs on the first antennae, the long flagellum of the second, and the longer caudal appendages. The **eggs** are carried by the female between the thoracic appendages, and undergo a partial segmentation. A three-limbed (nauplius) stage has been shown by Metschnikoff to exist in their development, but they are hatched almost in the form of the adult.

The Silurian family, Ceratiocaridae, resembled the Leptostraca in the possession of a bivalve shell, and the peculiar movable head plate, but their organization is too imperfectly known in other respects to establish the relationship.

Family **Nebaliidae**. *Nebalia* Leach, widely distributed, British ; *Nebaliopsis* G. O. Sars, blind or nearly so, from deep water, Southern ocean ; *Paranebalia* Claus, Bermudas ; *Nebaliella* Thiele, eyestalks developed, but without lenses or pigment, thoracic legs without epipodites ; shallow water, Kerguelen I. and N. Zealand.

Division 2. EUMALACOSTRACA.

Malacostraca with seven abdominal segments including the telson. They are without a shell muscle, and without a caudal fork in the adult.

Order 1. SYNCARIDA. Packard.*

Malacostraca without a carapace, and with all the thoracic

* Packard, A. S. On the Syncarida, *Mem. Nat. Acad. Sc. Washington*, iii (2), 1886. Thomson, G. M. On a Freshwater Schizopod (*Anaspides*) from Tasmania, *Trans. Linn. Soc.*, Zool. vi (1893), p. 285. Calman, W. T. On the Genus *Anaspides*, *Trans. R. Soc. Edinburgh*, 38, pt. iv (1896), p. 787. Id. on the Classification of the Crustacea malacostraca, *Ann. and Mag. of N. H.*, ser. 7, xiii (1904), p. 144. Id. On the Characters of the Crustacean Genus *Bathynella* Vejd., *Journ. Linn. Soc.*, Zoology, vol. xxvii (1899), p. 338.

segments distinct. The eyes are pedunculate, the thoracic legs flexed between the fifth and sixth segments and there are no oostegites forming a brood pouch.

Surviving in streams and freshwater pools at an elevation of over 4,000 feet on the summit of Mount Wellington and elsewhere in Tasmania, is a small crustacean measuring 1 to 1½ inches in length, which appears in many of its characters to have retained primitive features of the malacostracan stock. It was discovered and described in 1892 by G. M. Thomson, and the very interesting relations which it presents to other recent forms, and to palaeozoic Crustacea have been set forth by Calman. In shape it somewhat resembles the Amphipod *Gammarus*, though it is less flattened laterally.

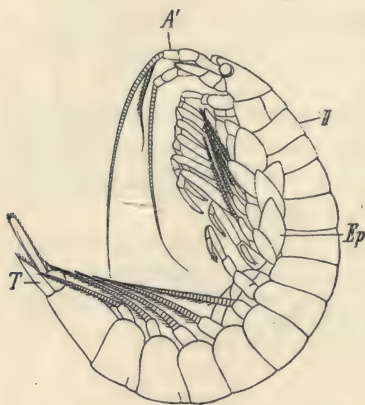


FIG. 286.—*Anaspides tasmaniae* (from Claus, after Calman). A' first antennae; II second thoracic segment; Ep epipodites; T telson.

There is no carapace, and the head is divided off by a transverse groove, which apparently marks the front limit of the thorax, though the forward slant of the lateral parts of the groove makes this conclusion uncertain. The head shield ends in a short rostrum in front, on either side of which are the stalked eyes.

The 1st antenna has a 3-segmented base and is biramous. A statocyst is present in its basal segment, as in the Decapods. In the male the inner

ramus is curved at the base and beset with hooks, recalling the prehensile antennules of some Entomostraca. The 2nd antenna has a small flattened scale-like exopodite. The mandible has a large palp, but is without a lacinia mobilis. Of the two maxillae the first resembles that of the Euphausiidae, but the palp is vestigial.

If the above-mentioned groove has been correctly interpreted as marking the limit between head and thorax, *Anaspides* is one of the few Malacostraca, in which the eight thoracic segments remain distinct. Their appendages are biramous, having an ambulatory endopodite (flexed between the 5th and

6th segment of the limb) and a strong many-jointed swimming exopodite (Fig. 287). The coxopodite bears on its outer surface two flattened ovate branchial epipodites which project forwards above the bases of the legs.

Before the discovery of this form Claus had arrived at the conclusion that the oostegites of the "Peracarida," and the branchiae of Amphipoda were both to be regarded as epipodial structures, which have taken up a position internal to the bases of the limbs. In *Anaspides* we now meet with them in the unmodified condition, and both serving as branchiae.



FIG. 287.—The first and second, left, thoracic limbs of *Anaspides*. A maxilliped; B first walking leg; *en* endite; *ep* epipodites; *ex* exopodite (after Calman).

The first *thoracic appendages* (Fig. 287 A), though formed in most respects on the same type as the others, possess two gnathobasic lobes on the inner side of the coxopodite, and have thus, to this extent, the character of maxillipeds. The exopodite is also much reduced. In the 8th both exopodite and epipodites are wanting.

The abdomen is powerfully developed and the exopodites of the pleopods are strong, many-jointed rami, though the endopodites are reduced to small rounded lobes. The endopodites of the two anterior pleopods of the male are however modified as copulatory organs after the manner of those of Decapods. The uropods are broad flattened appendages and form, with the telson, a powerful caudal fin.

Our knowledge of the internal anatomy is far from complete. A true median eye has not been recognized. There is median group

of dots on the dorsal surface of the head, of unknown function. The stomach is situated far forward in the thorax and there are some 18 slender "hepatic" diverticula. The heart is a long tube, tapering at either end, and the wide part lies between the middle and the posterior end of the thorax. The excretory organ has not been identified, nor has the position of the generative orifices been satisfactorily determined. The alleged position of the male orifice on the first abdominal segment, and that of the female between the 7th and 8th thoracic, would be exceptional among the Malacostraca, and in neither sex was the duct followed to its opening. Eggs 1 mm. in diameter have been found in the oviduct, yet no trace of brood lamellae has been found, and it is probable, therefore, that a series of free larval stages occurs in development.*

A group of small Crustacea, *Palaeocaris*, *Gamponyx* and *Acanthotelson*, from the Carboniferous and Permian rocks of the Old and the New Worlds, have been recognized by palaeontologists as occupying an isolated position among the Malacostraca, and have been classed by Packard in the group *Syncarida*. Calman pointed out that they "agree with each other and with *Anaspides*, and together with it stand apart from all other Crustacea whatsoever, in combining with the absence of a carapace, the presence of distinctly podophthalmate characters in antennules, antennae, and tail-fan" † *Palaeocaris* appears to have had biramous thoracic legs, but it is not clear that this was the case in the other genera, nor are the epipodial plates preserved in the fossil forms, hence these features so characteristic of *Anaspides* cannot at present be included in the definition of the *Syncarida* as a group.‡

Genus *Anaspides* Thomson. Tasmania.

* Since this was written *Anaspides* has been investigated afresh by Mr. G. Smith. The author has learnt from Mr. Smith that he has found the free-swimming young in the form of the adult of so small a size that he has no doubt that they are hatched essentially in this condition. It appears therefore that *Anaspides*, like *Astacus* and other freshwater forms, undergoes no considerable metamorphosis.

† Loc. cit., p. 796. The Malacostraca with stalked eyes have been classed in a group the Podophthalmata, in contrast with the Edriophthalmata, or sessile-eyed forms; an arrangement which is now generally abandoned.

‡ *Koonunga cursor* has recently been described by O. A. Sayce (*Victorian Naturalist*, vol. 24, No. 7 (Nov. 1907)). It is $\frac{1}{3}$ in. long and lives in fresh water pools, near Melbourne, Victoria. The thoracic legs are like those of *Anaspides*, but the eyes are sessile, and there is no scale to the second antenna.

Fossil Genera *Palaeocaris* and *Acanthotelson* Meek and Worthen, Coal Measures, Illinois, *Gampsonyx* Coal Measures, Saarbrück.

Bathynella natans, a minute crustacean, not exceeding 1 mm. in length, two specimens of which were obtained by Vejdovsky in well water in Prague, appears to be allied to *Anaspides*. An account of its anatomy, so far as a single ill-preserved specimen rendered it possible, is given by Calman (loc. cit.). There is no shield. The eight thoracic segments appear to be distinct and they carry biramous appendages, each with a single epipodial lobe. The uropods are well developed, and the most anterior pleopods are present, but the intermediate pleopods are missing. No trace of eyes was found.

Order 2. SCHIZOPODA.*

Small Malacostraca with a large and usually flexible cephalothoracic shield, and with the eight pairs of generally biramous thoracic legs of approximately similar form. The gills, when present, form a single series and project freely.

The name Schizopoda was introduced in 1817 by Latreille for a group of his Decapoda Macrura containing the two genera *Mysis* and *Nebalia*. The latter was separated in 1829, but during the next 50 years, as new species were discovered, many forms besides those now generally recognized as Schizopods were temporarily contained in it, and subsequently placed elsewhere. The Stomatopods and some of the lower Decapods were thus included, as well as a number of larval forms of Decapods, at

* C. Claus, *Unters. z. Erforschung d. genealogischen Grundlage d. Crustaceensystems*, Wien, 1876. Id. Neue Beiträge z. Morphologie d. Crustaceen, *Arb. aus d. Zool. Inst. Wien*, T. 6, 1886. Id. Zur Kenntniss der Kreislauforgane d. Schizopoden u. Decapoden, *Ibid.*, T. 5, 1884. G. O. Sars, *Hist. Nat. d. Crustacés d'eau douce de Norvège*, Christiania, 1867. Id. *Carcinologische Bidrag. til Norges Fauna. Mysider*, Christiania, 1870. Id. *Rep. on the Schizopoda collected by H.M.S. Challenger*, 1885. E. van Beneden, *Recherches sur l'embryogénie des Crustacés*, II, *Bull. Acad. Belgique*, 1869. E. Metschnikoff, Ueb. d. Naupliuszustand von Euphausia *Zeits. f. wiss. Zool.*, xxi, 1871. R. v. Willemoes-Suhm, On some Atlantic Crustacea, *Trans. Linn. Soc.*, 1875. J. Nusbaum, L'Embryologie de Mysis Chamaeleo, *Arch. Zool. exp.*, 1887. P. Butschinsky, Zur Entwicklungsgeschichte d. Mysiden, *Schriften d. neu-russ. Gesellsch. d. Naturforsch.* (Russ.), Odessa, 1890. R. S. Bergh, Beitr. z. Embryologie d. Crustaceen, I, *Zool. Jahrb.* vi (1893). J. Wagner, Unt. üb. d. Entw. d. Arthropoden, *Arb. Nat. Ges. Petersburg*, 1896. C. Chun, Atlantis, *Bibl. Zool.* xix, 1896. W. T. Calman, On the Classification of the Malacostraca, *Ann. and Mag. of Nat. Hist.*, ser. 7, vol. 13, 1904. E. W. L. Holt and W. M. Tattersall, Schizopodous Crustacea from the North-East Atlantic Slope, *Rept. on the Sea and Inland Fisheries of Ireland*, 1902-3, pt. II. No. IV, i. W. T. Calman, Note on a genus of Euphausiid Crustacea, *Ibid.* No. IV, ii.

first regarded as mature animals, which present features resembling those of the Schizopods, but lost by the adults.

The group Schizopoda as now understood has been generally accepted since 1861, either as subordinate to the Decapoda or as a distinct order. In either case the species included in it have been regarded as holding a central position among the Malacostraca and especially as leading on to the decapod series.*

In their outward appearance the Schizopoda resemble the long-tailed Decapods, inasmuch as they possess an elongated and usually compressed body, a large dorsal shield covering the thoracic segments more or less completely and a well-developed abdomen. In the structure of their anterior thoracic legs, however, they differ essentially from the great majority of adult Decapods and approach the more advanced larvae of the prawns, which they also resemble in their simpler internal organization.



FIG. 288.—*Mysis oculata* (from Claus, after G. O. Sars). Gb vesicular sense organ.

Further, in the Holotropha the dorsal shield leaves a greater number of the thoracic segments free.

The cuticle is generally thin, but in the Lophogastridae it is strongly calcified and rigid. The front of the cephalothorax is usually divided from the hinder part by a groove corresponding in position with the articulation of the mandible. A rostrum is usually present, long and spearlike in the Lophogastridae.

Appendages.—The first *antennae* end in two long flagella, the second in a flagellum and a large scale (exopodite). In the *mandible* a lacinia mobilis is present in the Holotropha, absent

* Cf. however p. 453.

in the Hemitropha (Fig. 280, p. 438). The first *maxillae* are usually small, two- or three-lobed plates, but in the Lophogastridae a small dorsally directed process ending in long setae is present, as in *Nebalia*, the Cumacea, and Chelifera. In this family also a large setose exopodial plate of the second maxilla is largely developed, homologous with the scaphognathite of Decapods.

The *thoracic appendages* are, as the name of the group implies, divided; having a leg-like endopodite and a many-jointed, setose, swimming exopodite, and though in the Holotropha one or

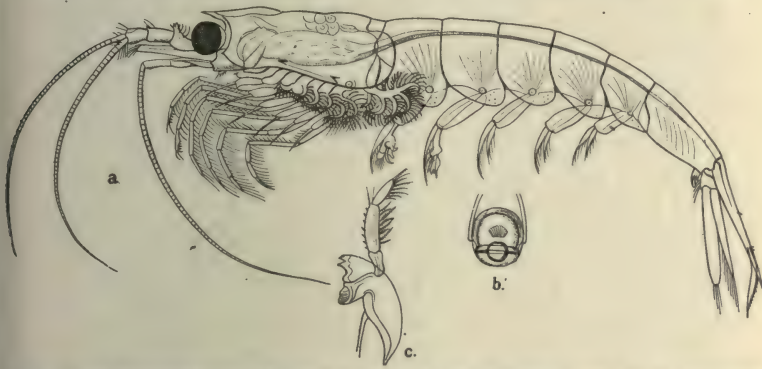


FIG. 289.—*Euphausia pellucida* (after G. O Sars). *a* the adult male \times about 8; *b* a luminous organ from the tail; *c* mandible.

more of the anterior pairs have taken on the character of maxillipeds, they form, as a rule, a uniform series, in contrast with differentiated condition found in the Decapods. There are two basal segments, to the first of which (Hemitropha) or to the arthrodial membrane connecting it with the trunk (Lophogastridae) the gills are attached, and the second supports the exopodite. In the Holotropha the epipodite of the 1st thoracic limb is a simple branchial appendage (cf. Chelifera and Cumacea). The Mysidae have no epipodial gills, apart from this appendage.

In *Gnathophausia* a small epipodial appendage on the distal side of the gill springs from the basipodite (Sars) and this, as Calman suggests, may possibly be the homologue of the gill of the Hemitropha (cf. p. 468). In the females of the Holotropha appendages of some of the thoracic legs, modified as *oostegites*, form the brood pouch, as stated below.

In some Mysidae lobed masticatory processes of the basal joint of the first pair resemble those found in the limbs of *Apus*. In

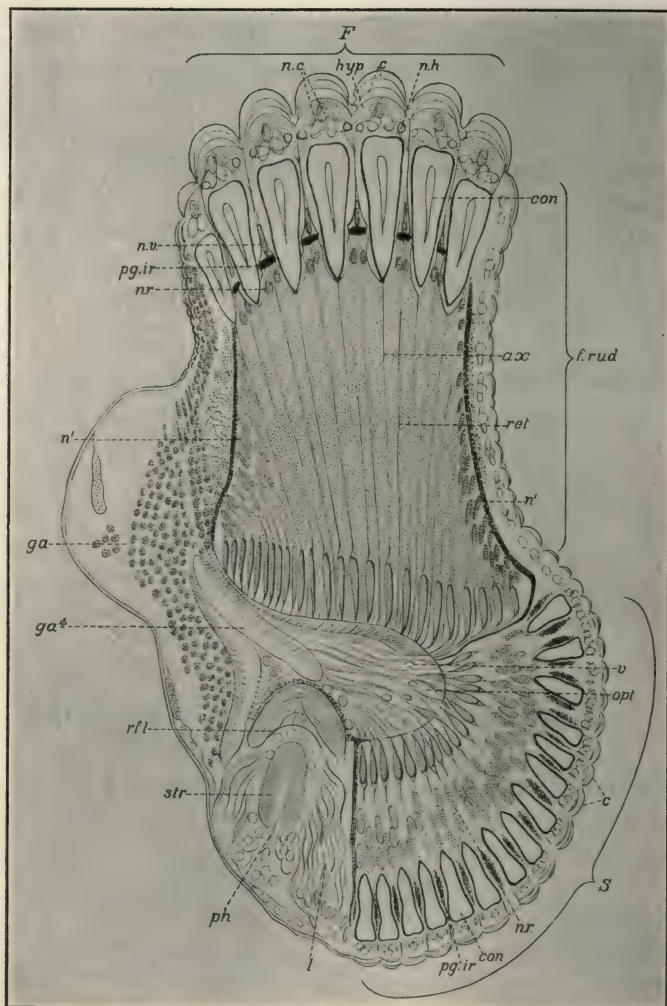


FIG. 290.—Section of the eye of *Stylocheiron* (after Chun). *ax* axial fibres; *c* cornea; *con* crystalline cones; *F* frontal eye; *f.rud* vestigial side-facets of frontal eye; *ga* ganglion cells; *ga⁴* distal optic ganglion; *hyp* hypodermal cells; *l* lamellae of the luminous organ in the eye stalk; *n'* nuclei of the reticular cells which correspond to the vestigial corneal facets of *f.rud*; *nc* Semper's nuclei; *nh* nuclei of hypodermal cells; *nr* retinal nuclei; *nv* nuclei of iris pigment cells; *opt* optic fibres; *pg.ir* iris pigment; *ph* luminous organ; *ret* retinula; *rfl* inner surface of reflector of the luminous organ; *S* lateral eye; *str* striated body (it is uncertain whether this or the reflector is the seat of the luminous substance); *v* blood-vessels.

some Euphausiidae the endopodite of the last pair (in *Euphausia* of the seventh and eighth) has disappeared, though the base remains bearing the gills and the minute exopodite. On the

other hand in the females of *Nyctiphanes* the exopodites are absent from the sixth and seventh pairs.

The five anterior *abdominal legs* are biramous swimmerets with a two-jointed base. An appendix interna is present on the endopodite in the Euphausiidae. The two anterior legs may be modified as accessory copulatory organs in the males of this family. In the male *Siriella* the endopodite bears peculiar branchial (?) processes. In the females of the Mysidae (Fig. 288) all the pleopods are reduced or absent (another Cumacean character). The sixth form with the telson a caudal fin, as in Syncarida, Stomatopoda and Decapoda.

The nauplius **eye** persists throughout life in some cases (*Euphausia*), and the stalked paired eyes are usually well developed, especially in the Hemitropha, which are also provided with luminous organs. In several genera of this tribe and also in some of the Mysidae, the compound eye is more or less completely divided into a frontal portion, with few but much enlarged elements, and a lateral (Fig. 290). Moreover, as shown by Chun * in the forms inhabiting great depths of the ocean (300–600 fathoms), illuminated only by phosphorescent light, retinal pigment is absent (cf. p. 333), while the pigment of the iris cells is disposed differently in the frontal and lateral divisions of the eye (*pg. ir*).

The **luminous organs** are spherical structures having, in their fully developed condition (Fig. 289 *b*), a transparent ‘cornea’ and lens in front of the lamellate body which is probably the source of light, and glistening pigment behind it. They are in many cases 10 in number, situated in the eye stalks (Fig. 290), the bases of the second and seventh thoracic legs, and in the median ventral line on the four anterior abdominal segments (Fig. 289). They are supplied with muscles by which they are turned in different ways, and emit a bright light either at the will of the animal or as the result of direct stimulation. They are among the many sources of the brilliant sparkles seen at night in the ocean.

A closed **otocyst** is present in the endopodite of the caudal appendages in most Mysidae (Fig. 288, *Gb*).

Fig. 241 *a* represents the **central nervous system** of *Euphausia*, which is remarkable for the distinctness of the neuromeres, but in *Mysis* the thoracic ganglia are more closely united.

* Atlantis, *Bibliotheca Zool.* Hft. 19.

The Hemitropha are in the adult provided with a large number of thin **hepatic tubes**, but in the larva, as also in the *Mysidae*, the number is smaller (5 or fewer pairs). There are no paired rectal diverticula.

An **antennal excretory gland** opening at the base of the second antenna has been recognized in *Mysis*.

The **heart** is tubular, with a slight anterior enlargement (cf. Stomatopoda) in *Mysidae*, but in the Hemitropha it is short and capsular, and situated in the hinder part of the thorax. Two or three pairs of ostia are present in either case.

Respiratory organs. In the Lophogastridae and *Mysidae* a simple elongated or ovate epipodial lobe is borne by the first thoracic legs, but the other thoracic legs in the Lophogastridae and also the thoracic legs of the Hemitropha bear subdivided gills.

The character of the gills differs considerably in the two families. In the Lophogastridae they each consist of a group of three or four bipinnate tufts, the segments of which are again pinnatifid, springing close together from the outer side of the arthrodial membrane of the seven posterior thoracic legs. They are therefore arthrobranchiae. Moreover in *Gnathophausia* a small setose lobe is also present arising from the basal segment of the limb, and is regarded by Sars as an epipodial structure. In the Hemitropha the gill is a branched rachis, the branches of which bear simple digitate lobes, and it is a podobranchia, springing from the outer side of the protopodite. In this family the size and the number of the branches of the gills increase from before backwards.

In the *Mysidae* there are no gills, unless in the genus *Siriella*, in which peculiar curved lobes, possibly of respiratory function, are borne on the endopodites of the abdominal appendages of the male. The appendage of the maxilliped found in this family and in the Lophogastridae, is during life kept in constant motion, and perhaps rather subserves respiration by means of the currents so set up over the surface of the body, than itself directly effects it.

The **oviducts** open as usual at the base of the sixth thoracic legs.

In accordance with the differences in the condition in which the young are hatched, a *brood pouch* is present in the Holo-tropha, but absent in the Hemitropha. It consists of lamellar processes (oostegites) from the bases of the two (*Mysis*) to seven (Lophogastridae) posterior thoracic legs.

In the Hemitropha the eggs are contained until hatching in a median or paired ovisac secreted by the oviducts. The

spermatozoa are filiform in *Mysis*, but in the Hemitropha they are elliptical cells and, as in the Decapods, are transferred to the female in spermatophores. In the Holotropha the vasa deferentia opens on conical eminences on the bases of the last thoracic legs. These projections are absent in the Hemitropha,

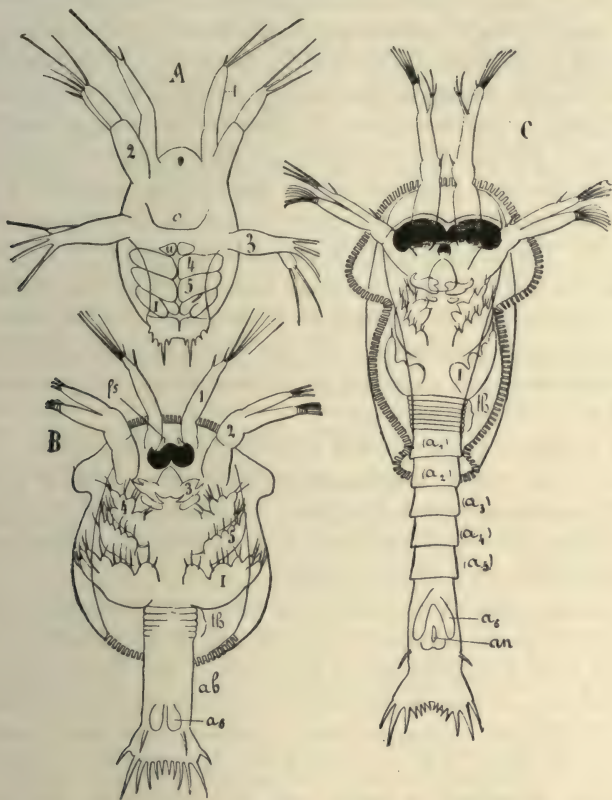


FIG. 291.—Three stages in the development of *Euphausia*. *A* metanauplius (after Metschnikoff); *B* Calyptopis stage (after Claus); *C* later Calyptopis stage (after Claus). 1 and 2, in *A* and *B*, first and second antennae; 3 mandible; 4 and 5 first and second maxillae; *I*, in *C*, first maxillipeds; *a*₁–*a*₅ first to fifth abdominal segments; *a*₆ sixth abdominal limbs; *ab* abdomen; *an* anus; *ps* frontal organ; *o* upper lip; *th* thoracic segments; *u* lower lip. (From Korschelt and Heider.)

but the two anterior pairs of abdominal feet are here modified as copulatory organs. In the Mysidae the males are distinguished by the full development of the swimmerets, and in *Siriella* by the presence on the latter of the peculiar branchial (?) appendages noted above. In all, the males are distinguished by the structure

of the first antennae, a peculiar tuft of hairs being present at the end of the shaft.

Development. The eggs of the Hemitropha hatch out, as shown by Metschnikoff (*Euphausia*), in the nauplius stage, having the usual character of the appendages, but with the eye and anus as yet undeveloped. In the course of their metamorphosis they pass through metanauplius, protozoaea and zoaea stages (Fig. 291), the latter (described by Dana as *Calyptopsis*) differing from the Decapod zoaea in possessing only one pair of maxillipeds. The margins of the shield of the larva are curiously serrated. Though the segments are formed in order from before backwards, the abdominal appendages begin to appear before the last thoracic, and their full number is completed first.

In the development of *Mysis*, which occurs in the brood pouch, the larva hatches in a stage corresponding to the nauplius. The nauplius skin is retained as an envelope within which the metamorphosis progresses. All the thoracic limbs are formed simultaneously. A caudal fork is present in the larva, as is usual in the Entomostraca.

All known Schizopods are inhabitants of salt-water except *Mysis relicta*, widely distributed in fresh-water lakes in Europe and N. America, and a few other Mysidae, which also live in fresh-water. Several forms allied to *Mysis* are indigenous to the brackish water of the Caspian.

Many are pelagic and often congregate near the surface of the sea in enormous numbers. The shoals of *Euphausia inermis* form the chief constituent of the food of the hump-back and other whales, which follow them in their movements during the summer months, accompanied by hosts of fish and birds. A species of *Mysis* furnishes food for the herring. They are especially abundant in arctic seas, but are widely distributed over the globe. *Gnathophausia*, many species of which were obtained in the voyage of the *Challenger*, inhabits deep water. A discussion of the systematic relations of the Schizopoda is given above (p. 453).

Tribe 1. HEMITROPHA.

First resemble the succeeding thoracic legs. Posterior part of dorsal shield not free from the underlying segments. Mandible without a lacinia mobilis. Heart short, polygonal. The eggs carried in ovisacs, and the young hatched as nauplii.

Fam. 1. **Euphausiidae (Thysanopodidae*)**. Cuticle thin; thoracic legs bear gills and the last or last two pairs are generally vestigial. No otolithic vesicle, but refracting luminiferous organs. Most species pelagic.

Sub-fam. 1. **Euphausinae**. Eyes not or only slightly bilobate; none of the legs much longer than their immediate fellows, nor ending in brushes or claws; palps of maxillae simple. *Euphausia* Dana, 7th and 8th legs vestigial; *Boreophausia* Sars. *B. inermis* (Kröy.), Arctic to English Channel. *Thysanopoda* M. Edw., only the 8th legs vestigial, the 7th like the 6th. *Nyctiphanes* Sars, only the 8th legs vestigial, the 6th and 7th without exopodites in female, peduncle of 1st antenna stouter in male than in female. *N. norvegica* M. Sars, British and other seas. *Meganyctiphanes* Holt and Tattersall, only the 8th leg vestigial, 6th and 7th with exopodites in both sexes, peduncle of 1st antenna scarcely stouter in the males.†

Sub-fam. 2. **Nematoscellinae**. Eyes more or less bilobate; 2nd or 3rd legs elongated, ending in a brush or claw. *Thysanoessa* Brandt, 2nd legs moderately elongated, last three gills two-branched. *Nematoscelis* Sars, 2nd legs much elongated with terminal group of spines, last five gills branched. *Stylocheiron* Sars, 3rd legs elongated, with a more or less perfect chelate "hand," gills much reduced. *Nematobranchion* Calman, 3rd legs elongated, with a terminal group of spines.

Sub-fam. 3. **Bentheuphausinae**. Eyes imperfect, none of the legs much longer than their fellows, palps of maxillae three-segmented. *Bentheuphausia* Sars, without luminiferous organs. *B. amblyops* Sars, abysses of Southern Ocean and Bay of Biscay.

Tribe 2. HOLOTROPHA.

First thoracic feet modified as maxillipeds, and bearing a simple branchial epipodite. Posterior part of the dorsal shield only overlaps the thoracic segments. Mandible with a lacinia mobilis. Heart tubular. Young developed in a brood pouch and becoming free in the adult form.

Fam. 1. **Mysidae**. Cuticle thin and transparent; edges of the dorsal shield not overlapping the base of the limbs; thoracic legs (except the 1st) without gills; otolithic vesicle usually present in caudal appendage; brood lamellae usually confined to the two or three posterior thoracic legs. Abdominal swimming feet vestigial in female. *Mysis* Latr., many species, one British; *Hemimysis* Sars; *Leptomysis* Sars. The following 5 genera, closely allied to *Mysis*, are indigenous in the brackish waters of the Caspian Sea: *Paramysis* Czern.; *Metamysis* Sars; *Mesomysis* Czern.; *Katamysis* Sars and *Limnomysis* Czern. *Austromysis* Czern, occurs in the Mediterranean and the Caspian. *Podopsis* Thomps.; *Amblyops* Sars; *Pseudomma* Sars, blind; *Erythrops* Sars; *Hypererythrops* Holt and Tattersall; *Euchaetomera* Sars; *Meterythrops* Smith; *Katerythrops*, *Paramblyops* and *Dactylerythrops* Holt and Tattersall; *Arachnomysis* Chun; *Chunomysis* Holt and Tattersall; *Brutomysis* Chun; *Parerythrops* Sars; *Caesaromysis* Ortmann; *Mysidopsis*, *Mysideis* and *Mysidella* Sars; *Heteromysis* Smith, abdominal legs of male small as in female. Littoral. *Gastrosaccus* Norm.; *Haplostylus* Kossm.; *Anchialis*

* So named from the character of the branchiae (*θυσανος*, a tuft).

† The genera named by Holt and Tattersall in this and the following Tribe have been obtained by these authors from the Atlantic slope to the W. of Ireland.

Kröy.; *Petalophthalmus* W.-Suhm. *P. armiger*. Male with greatly developed mandibular palp, and small dorsal shield. Eyes blind, curved and flattened. N. Atlantic, 100–2,500 fathoms. *Boreomysis* Sars, deep sea; *Siriella* Dana, thoracic appendages with claws, endopodites of abdominal legs with peculiar spirally curved (branchial ?) processes. Pelagic.

Fam. 2. **Lophogastridae**. Cuticle calcified; thoracic legs bear gills, and their bases are covered by the edges of the dorsal shield; otolithic vesicle absent, brood lamellae on seven thoracic legs. *Lophogaster* M. Sars, rostrum short, antennal scale broad. *L. typicus* M. Sars, a bottom form in N. and S. Hemispheres. *Ceratolepis* Sars. *Gnathophausia* W.-Suhm, rostrum long, spear-like, outer flagellum of anterior antennae as long as body. Several spp. from deep sea. *G. ingens* Dohrn, attains a length of over 6 in. from tip of rostrum to that of telson. *G. drepanephora*, off W. coast of Ireland; *Chalaraspis* Sars, dorsal shield overlaps the anterior abdominal segments. One specimen from 1,800 fthms. S. Ocean. *Eucopia* Dana. *E. australis* Dana. Four anterior thoracic appendages modified as maxillipeds, the three succeeding pairs very long and directed forwards. All seven armed with a small prehensile claw; 8th shorter. Widely distributed in deep water.

Order 3. CUMACEA.*

Malacostraca with a small cephalothoracic shield and four or five free thoracic segments, the first, second and third thoracic limbs are maxillipeds, the first bearing respiratory lamellae, and two or more succeeding pairs of legs are biramous; the abdomen is slender and elongated, and generally bears, in the male, two to five pairs of swimming feet besides the caudal (6th) appendages, which are alone present on it in the female.

The Cumacea are small marine animals frequenting the neighbourhood of muddy and sandy shores, though they extend also into deep water. For our knowledge of their anatomy we are mainly indebted to G. O. Sars. They are in many respects intermediate in character between the Amphipoda and Isopoda on the one hand, and the Schizopoda on the other.

The integument is firm and brittle, and the body divided

* H. Kröyer, Om Cumaceernes Familie, *Naturh. Tidsskr.*, 1846. A. Dohrn, Ueber Bau u. Entw. d. Cumaceen, *Jen. Zeits.*, T. v, 1870. H. Blanc, Dev. de l'oeuf et formation d. feuillets primitifs chez la Cuma Rathkii, *Rec. Zool. Suisse*, II, 1885. H. J. Hansen, *Isopoden, Cumaceen u. Stomatopoden d. Plankton-Expedition*, 1895. G. O. Sars, *An account of the Crustacea of Norway*, III, *Cumacea*, Bergen, 1900. Calman, W. T. The Marine Fauna of the W. Coast of Ireland, pt. IV, *Cumacea, Fisheries, Ireland, Sci. Invest.*, 1904, I (1905). Id. *Cumacea of the Siboga Exped.* Leiden, 1905.

into regions which correspond approximately with those found in the Stomatopods.

The oval cephalothorax includes the three anterior thoracic segments. It is produced laterally into folds fitting closely at the margins, including a respiratory chamber on either side.

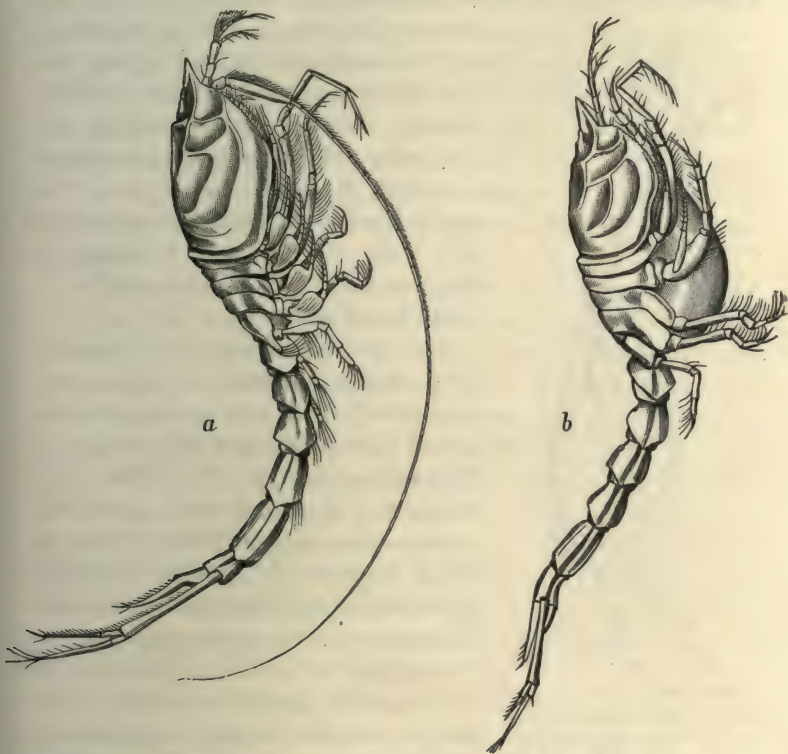


FIG. 292.—*Diastylis sculpta*. *a* male, and *b* female (from Claus).

Anteriorly the sides of the cephalothorax extend forwards and (except in *Stephanomma*) meet one another, forming a bi-partite pseudo-rostrum in front of the rostrum proper. The eyes, when present, are situated on the latter. The surface is smooth in the males but frequently spiny in the females and produced into ridges.

The long abdomen is capable of being bent forwards, either ventrally or dorsally, the latter movement having suggested the name *Oniscus scorpioides*, under which Lepechin gave the first.

description (1780) of a member of the order. A dagger-shaped telson projecting beyond the sixth segment, may or may not be present. The anterior *antennae* are short and biramous. The posterior are uniramous, short and, in many cases, unsegmented in the female, while in the male a multiarticulate flagellum beset with sensory hairs and equalling the body in length is borne on a five-jointed shaft of the appendage.

The *mandible* is without a palp. The two-lobed first *maxilla* has a backwardly directed process bearing two long setae, which lie in the respiratory chamber, in which feature, as in the elongation of the posterior antennae of the male, the Cumacea resemble the Leptostraca. The second maxilla is a small lobed plate.

The first *maxilliped* of the Cumacea (Fig. 293) is modified in relation with a peculiar form of respiratory apparatus which finds its parallel only among the Tanaidacea (see p. 478). The main ramus is a short and stout setose limb, in apposition with its fellow. From its basal segment a large scoop-shaped appendage (*pp*) projects upward and backward into the respiratory chamber, bearing on its inner margin a number of branchial lamellae, which lie in the hollow enclosed between the appendage and the thoracic wall. Further, from the base of the maxilliped another process (*ap*) extends forward, which curves

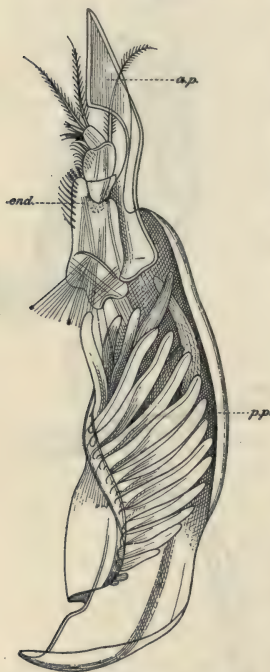


FIG 293 —Right first maxilliped of *Diastylis stygia* seen from above (after Sars). *a.p.* anterior and *p.p.* posterior process from the base of the appendage; *end* basal segment bearing the endopodite.

round to meet its fellow in front of the labrum under the front of the head, and with the adjoining parts, forms a channel through which water, driven by the scoop-shaped plate, is directed forwards from the branchial chamber. It would appear that these processes must be regarded as epipodites. The posterior, in the combination of branchial filaments with a plate-like lobe, recalls the podobranchia of *Astacus*. Other branchial structures are absent in the Cumacea.

The second maxillipeds are intermediate in character between the first and the succeeding appendages though they are without exopodites. In adult females they bear at their bases short fan-shaped appendages which lie at the anterior limit of the brood chamber, and, apparently, promote the respiration of the young.

Of the *remaining six thoracic limbs* two to five of the anterior pairs bear well-developed setose exopodites, springing from the basal joint, by means of which the animals swim. The number of these appendages which are biramous, is greater in the male than in the female. In the abdomen, again, the uropods are alone present in the females, as long and stiff biramous structures, beset with setae like the teeth of a comb, but in the males, short *swimming feet* are generally found on some of the anterior segments

In the **central nervous system** each of the postoral segments (17) is represented by a ganglion. In comparison with other Malacostraca, the Cumacea are very poorly provided with organs of vision. When present at all the **eyes** form a median group (paired in the larva, and in *Nannastacus* in the adult) of pigment spots, with several small refracting lenses, situated on the rostrum. They are probably to be regarded as paired eyes, which have become approximated.

In the **alimentary canal** a masticatory stomach and generally three pairs of hepatic tubes are present. In *Platycuma Holti* Calman has recently described (loc. cit.) a long coiled tract of the alimentary canal (stomodeal ?)—a most exceptional condition in Crustacea.

The **heart** is oval and lies in the anterior free thoracic segments, and the adjoining part of the cephalothorax. A convoluted **shell gland** is present in the neighbourhood of the second maxilla. The orifices of the **oviducts** have not been recognized, but the vasa deferentia open as usual on the last thoracic segment, and the spermatozoa are filiform. A brood pouch is formed in the breeding season by paired over-lapping lobes beneath the fourth, fifth and sixth (the first three free) thoracic segments. The relation of these lobes to the epipodial oostegites of other Malacostraca has not been satisfactorily determined.

The males of the Cumacea are found at night, swimming in shoals, from which females are absent. The females on the other hand are found more abundantly in sand on the bottom.

Corresponding with this difference in habit there is a well marked sexual dimorphism, the males having the carapace smooth, long posterior antennae, and the differences in the thoracic and abdominal appendages noted above. None of the appendages of the male are modified as copulatory organs.

The young of the Cumacea are hatched in the form of the adult, except that the eighth thoracic feet are absent, in which as in other features of their development they resemble the Isopoda.

The arctic seas, up to the edge of the perpetual ice, are especially rich in genera and species of Cumacea and here too and in deep water elsewhere they attain their largest size (35 mm.) They also occur in the antarctic seas, but appear to be scarce in shallow tropical waters. They have been taken from a depth of 2,600 fathoms. The free-swimming shoals are the prey of shoals of herring. Together with species of Mysidae and other relicts of a marine fauna the Cumacea are represented by several species in the salt waters of the Caspian Sea.

No fossil forms are known.

The Cumacea are arranged in the following nine families by G. O. Sars.

Fam. 1. **Cumidae**. Carapace comparatively large; thoracic appendages 5-8 without exopodites in both sexes; 5 pairs of pleopods in male. Telson absent. *Cuma* M. Edw.; *Iphinoë* Sp.B.; *Cyclaspis* G.O.S.; *Cyclaspoides* Bonnier; *Cumopsis* G.O.S.; *Stephanomma* G.O.S.

Fam. 2. **Vaunthompsoniidae**. General form as in Cumidae, but exopodites are present on thoracic legs 2-4 in the female, 2-5 in the male. *Vaunthompsonia* Sp.B. 2 spp. known one British (*V. cristata*) the other from Kerguelen. *Leptocuma* G.O.S.; *Heterocuma* Miers; *Bathycuma* Hansen.

Fam. 3. **Lampropidae**. Carapace generally rather small; exopodites on thoracic legs 4-7; pleopods not more than 3 in the male. Telson well developed. *Lamprops* G.O.S.; *Hemilamprops* G.O.S.; *Paralamprops* G.O.S.

Fam. 4. **Platyspididae**. Resembles the last, but the carapace very large and flattened, and thoracic appendages 5-8 without exopodites in the male. *Platyspis* G.O.S.; *Chalarostylis* Norm.

Fam. 5. **Leuconidae**. Carapace small; thoracic appendages 4-7 with exopodites; only two pleopods in the males; telson absent. *Leucon* Kröyer; *Eudorella* Sp.B.; *Eudorellopsis* G.O.S.

Fam. 6. **Diastylidae**. Head and thorax tumid, abdomen abruptly narrowed, with freely moving nodular segments and a long distally tapering telson. Thoracic appendages 4-5 in female, 4-7 in male with exopodites, 2 pleopods in male, uropods long and slender. *Diastylis* Say, some 30 known spp. (Fig. 292). *Diastylodes* G.O.S.; *Diastylopsis* S. Smith; *Leptostylis* G.O.S.; *Pachystylis* Hansen. *Pseudodiastylis* and *Paradiastylis* Calman.

Fam. 7. **Pseudocumidae**. Resembles Diastylidae and Lampropidae, but the telson is very small and flap-shaped, and the inner rami of the uropods are unsegmented. *Pseudocuma* G.O.S., 1 sp. found in the Caspian Sea; *Petalosarsia* Stebbing; and the 4 following hitherto only known from the Caspian: *Pterocuma* G.O.S.; *Stenocuma* G.O.S.; *Schizorhynchus* G.O.S. and *Caspiocuma* G.O.S.

Fam. 8. **Nannastacidae** (= **Cumellidae**). Telson and pleopods absent; thoracic appendages 4-7 with exopodites in the males. *Nannastacus* Sp.B. with paired eyes; *Cumella* G.O.S. with a median eye.

Fam. 9. **Campylaspidae**. Carapace very large depressed in front, vaulted behind; endopodite of 1st thoracic appendage (1st maxilliped) rudimentary. *Campylaspis* G.O.S.

Order 4. TANAIDACEA (CHELIFERA).*

Malacostraca with a cephalo-thorax formed by the fusion of the two anterior thoracic segments with the head, and produced on each side into a fold forming a respiratory chamber. The second thoracic limbs end in large chelae, and the abdominal appendages are lamellate and natatory.

The small Crustacea belonging to this order, occupy an intermediate position between the Cumacea on one hand and the Amphipods and Isopods on the other.

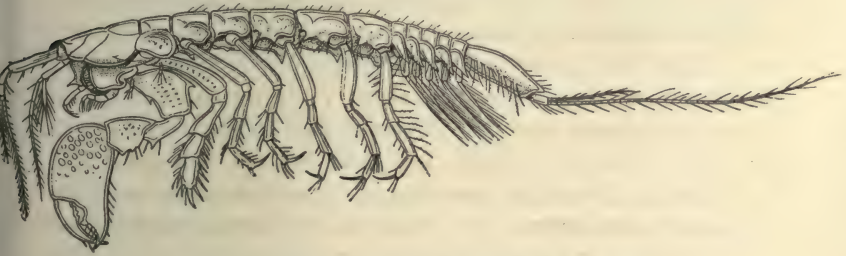


FIG. 294.—*Apseudes spinosus* (from Claus, after G. O. Sars).

The body is elongated and nearly cylindrical. The second thoracic segment which in most Amphipods and Isopods is the first free one is here, as in the Laemodipoda, united with the head to form a cephalothorax, the sides of which are produced into two folds, enclosing a respiratory chamber. The eyes, when present are raised on short stalks but are not mobile. The first antennae are biramous in *Apseudes*, uniramous in *Tanais* and

* Claus, Ueb. *Apseudes latreillei* und die Tanaiden. Claus' *Arbeiten*, T. v and vii. Sars, *Crustacea of Norway*, Isopoda.

its allies. In the latter genus, according to Fritz Müller, they bear at their bases *otocysts*, as in *Anaspides* and the Decapods, though this observation has not been confirmed by later writers. The second antennae bear in *Apseudes* an oval scale-like exopodite, recalling that of *Anaspides* and the Stomatopods. The *mandibular palp* may be present (*Apseudes*) or absent (*Tanais*). The first *maxilla* bears a backwardly directed setose flagellum at the base of its outer lamella as in Cumacea and the Leptostraca and the Lophogastridae. The second may be small or absent. Attached to the base of the *maxillipeds* is a stalked, scoop-shaped, membranous appendage which lies in the respiratory chamber, and is evidently homologous with the epipodial plate of the maxilliped in the Isopods and Holotrophous Schizopods, and apparently with the posterior plate of this appendage in the Cumacea. It does not appear that this, or any other structure of the Tanaidae is a true branchia, but by its movements and that of the flagellum of the first maxilla, water is kept flowing through the respiratory chamber, in the outer wall of which the blood circulates in a large sinus.

The second *thoracic limbs* end in powerful chelae, like those of the next pair but one in the Decapods. In *Apseudes* the third pair is large and fossorial. In this genus also, both second and third pairs bear minute exopodites at their bases (Fig. 294, cf. Cumacea). With the exception of the oostegites, mentioned below, epipodites are absent from the seven posterior thoracic limbs. As in Amphipods and the Phreatoicidae among the Isopods the three posterior thoracic legs are directed forward. The five anterior *abdominal appendages* (their number may be reduced) are natatory. They resemble one another and consist of two simple flattened setose lobes borne on a basal joint. The sixth are filiform and project beyond the hind end of the body. In these features the Chelifera resemble the Isopods, but the abdominal appendages are not modified as branchiae, as in that order. In accordance with the position of the paired respiratory chamber in the anterior part of the thorax, the **heart** also is thoracic, and it does not supply arteries direct to the abdominal appendages, as it does in Isopods (Delage).

A **shell gland** is present on the second maxilla (Claus). In some cases **sexual differences** in the shape of the first two pairs of legs and in other features may be marked.

The eggs undergo their development in an incubatory pouch formed by one (*Tanais*) or more pairs of oostegites developed from the ventral thoracic region. The embryos are dorsally flexed during their development, as in the Isopoda. The last thoracic, and all but the last abdominal appendages are absent in the newly hatched larva, as in the Cumacea.

In *Tanais dubius* (?) Kröyer, from the coast of Brazil, according to Fritz Müller, the males resemble the females until the last moult. After this they apparently cease to feed, the mouth appendages being lost, and in respect of their secondary sexual characters appear under two forms. In one, which is more abundant, they bear some 12 to 17 olfactory hairs on the anterior antennae, and have large and very mobile chelae, for holding the female, while the others are provided with chelae resembling those of the female, but are more richly equipped with olfactory hairs.

The Tanaidacea live on the bottom of the sea, in mud, frequently in tubes formed of agglutinated particles, from shallow water to a depth of over 1,000 fms.

Fam. 1. **Tanaidae.** *Tanais* named by M. Edw. (subgenera *Heterotanais*, *Typhlotanais*, *Leptognathia*, *Tanaopsis*, *Cryptocope*, *Haplocope*, *Strongylura*, *Anathrura*, *Pseudotanais* all G. O. Sars, *Paratanais* Dana) antennae simple, mandibular palp absent; 2nd, 3rd and 4th legs nearly alike, and the sixth abdominal leg short.

Fam. 2. **Apseudidae.** *Apseudes* Leach, eyes sessile, anterior antennae biramous, the posterior bearing an outer setose lobe, mandibular palp present, 3rd thoracic leg large, the uropods elongated. Related genera *Parapseudes* G. O. Sars, and *Sphyrapus* Norman and Stebbing.

Order 5. ISOPODA.*

Malacostraca without a carapace and usually with broad and somewhat flattened body, with seven free thoracic rings and with

* H. Rathke, *Untersuchungen über die Bildung und Entwicklung der Wasserassel*, Leipzig, 1832. Cornalia and Panceri, *Osservazione Zool. Anat. Sopra un nuovo genere de Crustacei Isopodi sedentarii*, Torino, 1858. A. Dohrn, Die Embryonalentwicklung des Asellus aquaticus, *Zeitschr. für wiss. Zool.*, Tom. xvii, 1867. N. Bobretzky, Zur Embryologie des Oniscus murarius, *Zeitschr. für wiss. Zool.*, Tom. xxiv, 1874. R. Kossmann, Die Entonisciden, *Mitth. Zool. Stat. Neapel*, iii, 1882. R. Walz, Ueber die Familie der Bopyriden, etc., *Arb. aus dem Zool. Inst., etc., Wien*, T. 4, 1882. Schiödte, J. C. and Meinert Fr. *Symbolae ad Monographiam Cymothoarum, etc., Nat. Tidskrift.*, xii and xiii, 1879-83. F. E. Beddard, *Report on the Isopoda collected by H.M.S. Challenger*, London, 1884-6. A. Giard et J. Bonnier *Contrib. à l'étude des Bopyriens, Trav. de l'Inst. Zool. de Lille*, T. 5, 1887. Id. *Contrib. à l'étude des Épicarides, Bull. Scient. de la France et de la Belgique*, 1895. J. Bonnier, Les Bopyridae. *Trav. Stat. Zool. Wimereux*, T. viii, 1900. H. J. Hansen, Cirolanidae et

lamellar legs, whose inner rami serve as branchiae, on the short-ringed, often reduced abdomen.

The body is flat and covered by a firm, usually calcareous integument, and presents in its structure a great agreement with that of the Amphipoda. The abdomen is, however, usually much shortened and the segments are often fused with one another forming a large caudal shield. The endopodites and sometimes also the exopodites of the abdominal legs are modified as branchial lamellae.



FIG. 295.—*Asellus aquaticus* (after G. O. Sars). Female with brood pouch, seen from the ventral side.

Isopods are in great part littoral Crustacea though some species (remarkable for their large size, and development of spines, Beddard) inhabit the bottom of the sea at great depths, others (e.g., *Asellus*) are inhabitants of fresh waters, and one group, the Oniscidae, is terrestrial. Besides these free-living forms many are parasitic on the bodies of fishes and Crustacea and in their structure and mode of life depart in varying degrees from the type of the free living forms, which however always recurs in the larval stages.

The anterior antennae are, with a few exceptions, shorter than the posterior and external antennae; in rare cases (Oniscidae) they become so much reduced that they are hidden beneath the cephalic shield.

As in the Amphipoda delicate plumose setae and olfactory

familiae nonnullae propinquaе, *Vid. Selsk. Skrift.* Kjöbenhavn, 1890. J. Nusbaum, *Materialien zur Embryogenie u. Histogenie d. Isopoden*, *Abh. Akad. Krakau*, 1893 (Polish). J. H. Stoller, *On the organs of respiration of the Oniscidae*, *Bibl. Zool. Heft*, xxv, 1899. G. O. Sars, *Hist. Nat. d. Crustacés d'eau douce de Norvège*, Christiania, 1867, and *Crustacea of Norway*, vol. ii., Isopoda, 1896-99. G. Smith, *Fauna u. Flora des Golfes von Neapel*, Monog. 29, Rhizocephala, 1906, etc.

vesicles are present on the antennae, but both anterior and posterior are uniramous. The *mouth parts* are generally masticatory, but in the parasitic forms they are suctional, and depart more or less from the typical condition here described. The *mandibles* bear a three-jointed palp, only wanting in Oniscidae, Bopyridae, and some other cases. The first *maxilla* is, on the other hand, without a palp and consists of two lobes, connected by a basal "cardo," and the second is plate-like and produced into four or fewer lobes. The closely united *maxillipeds* borne on a common basal piece (Fig. 296) form a structure like the labium of insects limiting the space about the mouth posteriorly. Each half consists of a basal segment (*stipes*) bearing externally the 5- or fewer jointed palp, and produced into a *lamina*, which may be connected with its fellow by interlocking hooks. A large epipodial (?) plate (*v*) is connected with the outer side of the stipes.

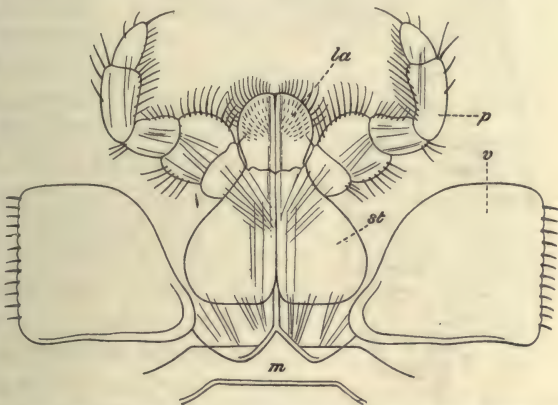


FIG. 296.—Maxilliped of *Asellus aquaticus* (after Gerstaecker). *la* lamina; *m* sternite of first thoracic segment; *p* palp; *st* "stipes"; *v* epipodial (?) plate.

The seven succeeding pairs of *thoracic legs* are, as a rule, adapted for walking or attachment, while the *abdominal appendages* are here modified in varying number, to serve as respiratory structures. When so modified, they consist of a basal segment supporting two rounded lobes, of which the inner has a delicate wall permitting the oxidization of the blood, while the outer, which protects it, is of firmer consistency. An anterior pair often forms an *operculum* (e.g. *Asellus*), while the 6th pair are frequently styliform or natatory; but in the Idotheidæ the latter are valvular, folding like doors over the other abdominal appendages. In the deep-sea form *Anuropus* they are respiratory like the preceding appendages. In another deep-sea form, *Bathynomus giganteus*, there

are branched outgrowths from the margins of the endopodites of the pleopods, increasing the respiratory surface. In the parasitic Bopyrina the pleopods may be reduced to simple plates, or, as in *Ione*, produced into long filiform and, in the female, branched appendages.

Finally, among the terrestrial Oniscidae, some genera (*Porcellio* and *Armadillium*) have acquired the power of breathing air, the exopodites of two or more of the anterior abdominal limbs being penetrated by numbers of minute tubular air spaces (Fig. 297), open-

ing at a notch on the outer margin, and causing a shining white patch visible to the naked eye; the endopodites of some of the limbs meanwhile retain the delicate lamellar character, enabling the animal, while in moist places, to breathe oxygen in solution.

The **central nervous system** resembles that of the Gammaridae among the Amphipods. In *Oniscus* the nerves to the mouth parts arise from the oesophageal commissure.

Eyes are usually present and consist of few or many elements, grouped together, in varying degrees of closeness, but they differ from those of the Amphipoda in the fact that each element is provided with a lenticular cornea. Thienemann* has

shown that a pair of **otocysts**, each opening by a narrow orifice to the exterior, is present in the telson of *Anthura*. In the nearly allied *Paranthura* they are absent.

The **alimentary canal** in most cases resembles that of the Amphipods, but rectal diverticula are not present in Isopods.

* Statocysten bei *Anthura gracilis*, *Zool. Anzeiger*, xxvi. (1903), p. 406.

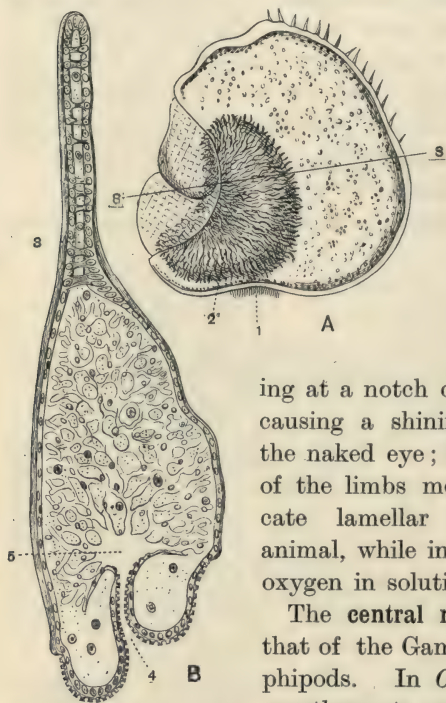


FIG. 297.—Exopodite of first right abdominal appendage of *Porcellio scaber*. *A* from the dorsal side, *B* in section along the line *s-s* in *A* (after Stoller). 1 articulation of exopodite with protopodite; 2 the "respiratory tree"; 3 blood cavity; 4 opening of the respiratory tree; 5 its cavity.

In the parasitic *Hemioniscus* and *Cryptoniscus* the alimentary canal ends blindly in the adult state, in a bilobed sac produced by the dilatation of two of the hepatic tubes.

Excretory organs. A small antennary gland has been recognized in the base of the first antenna, and a *shell gland* in the maxillary region.

The **heart** differs from that of Amphipods in its more posterior position, being largely contained in the abdomen, in ending blindly behind, and, in many cases at any rate, in giving off lateral arteries direct to the limbs.

Reproduction. In the great majority of Isopods as in most other Crustacea, the sexes are separate, and in shape and size the male and female are alike, but in association with the parasitic, and hence more or less stationary habit, we meet with two departures from the rule—*hermaphroditism*, and strongly marked *sexual dimorphism*. In the usual condition three tubular lobes of the testis on either side of the male unite to form a dilated seminal vesicle from which the vas deferens passes to a cylindrical or papilliform paired (*Asellus*) or single (*Oniscus*) penis, at or near the middle line on the last thoracic segment. The second abdominal appendages of the male are, moreover, provided with styliform processes from their inner borders.

In the female the simple tubular ovaries communicate laterally with oviducts which open on the sixth thoracic segment. *Oostegites*, arising close to the bases of the limbs of from two to six of the thoracic segments, form a brood pouch.

The female genital apertures often appear only at the time of formation of the brood pouch.

The phenomena of fertilization and the production of the brood in the Oniscidae, as described by Schöbl* are very remarkable. According to this author the two receptacula, which are invaginations of the outer integument into the mouths of the oviducts, are at first not in open communication with the latter. Only after sperm has, during copulation, entered the receptacula, does it enter the oviducts by the bursting of the walls separating them from the receptacula and thus bring about the fertilization of the eggs in the ovaries. The animal then casts its skin, and with the skin the receptacula seminis. The two genital apertures are now no longer present. The fertilized eggs pass from the ovaries into the body cavity and thence through a newly-formed, unpaired, birth aperture in the last thoracic

* J. Schöbl, Ueb. d. Fortpflanzung isopoder Crustaceen, *Arch. f. mikr. Anat.*, Bd. xvii (1880), p. 125.

segment but one, into the brood cavity. A new batch of eggs is fertilized later in the ovary by sperm left over from the first copulation, and this reaches the brood cavity in the same way. After this second batch of eggs has been developed in the brood cavity and the young that are hatched have left it, the animal moults, and then again appears as it was before copulation. (Lang.)

In *Sphaeroma rugicauda* the greater part of the development of the young occurs, not in the brood space but in four paired

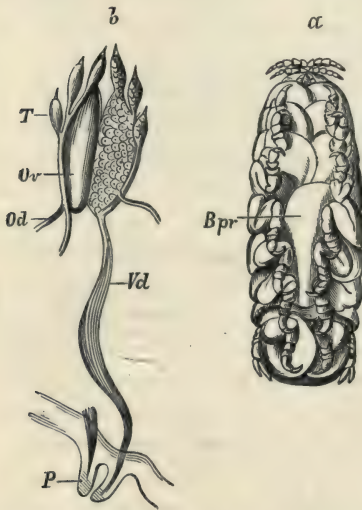


FIG. 298.—a Female phase of *Cymothoa Banksi* (after M. Edwards). Bpr oostegite. b sexual organs from a young *Cymothoa oestrices* (after P. Mayer). Od oviduct; Ov ovary; P penis; T the three testes; Vd vas deferens (from Claus).

brood sacks, formed by invagination of the ventral wall of the thorax and lying within the body. The young must enter these sacks soon after the eggs are hatched.*

Among the Cymothöina which are parasitic in the mouth and branchial cavities of fishes, three genera (*Cymothoa*, *Anilocra* and *Nerocila*) have been found to be hermaphrodite, † being male when young and acquiring female characters at a later period.

In the young stage they possess three pairs of testes, two rudimentary ovaries internal to the testes, a paired copulatory organ into which the two vasa deferentia open (Fig. 298), and the styliform processes of the male on the second abdominal legs. In the course of further growth, including two moults, the testes diminish and the external male organs disappear, while the ovaries develop and oostegites grow out from the ventral surface. Henceforward the animal is female. Many Epicaridea are similarly hermaphrodite; they are referred to below in relation with the metamorphosis of Isopods.

The embryonic development begins after the entry of the eggs

* Leichmann. *Bibl. Zool.* Hft. 10.

† J. Bullar, The generative organs of the Parasitic Isopoda, *Journ. Anat. Physiol.*, 1876. P. Mayer, Ueber den Hermaphroditismus einiger Isopoden, *Mittheil. aus der Zool. Stat. Neapel*, 1879.

into the brood pouch, and is introduced by a centrolecithal segmentation, the central part of the egg (food yolk) remaining at first unsegmented. The blastoderm soon consists of a peripheral layer of nucleated cells and produces by a rapid growth of its constituent cells the ventrally placed germinal bands, at the anterior end of which the cephalic lobes are first marked off. In *Asellus* two lobed prominences arise as paired appendages of the dorsal part of the thorax and shortly disappear. These are known as the "dorsal organ," but their nature is problematical. Of the appendages the two pairs of antennae and the mandibles are first formed in *Asellus* (Boas) and *Ligia* (Nusbaum), and after these have made their appearance a new cuticle, corresponding to that of the nauplius stage of other Crustacea, is separated, and envelops the embryo until it is hatched. While however the separation of this nauplius skin is of frequent occurrence among Isopods, the formation of the limbs in *Cymothoa* and *Oniscus* is simultaneous, with the exception of the last thoracic legs. These do not appear in the Isopoda until after the embryo has been hatched for some time. The caudal extremity is bent towards the dorsal surface during development.

Metamorphosis. Besides the development of the last (eighth) thoracic legs not inconsiderable changes occur in the form of the appendages before the attainment of sexual maturity. Hence the Isopoda may be said to undergo a metamorphosis. Among some of the parasitic forms it is of a very marked character. While the modification of structure in relation to the parasitic habit is comparatively slight in the Cymothoina and Aegina, the Epicaridea present a series of modifications which culminate

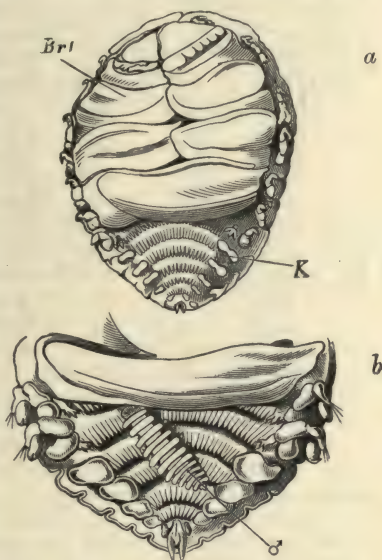


FIG. 299.—*Gyge branchialis*. *a* female seen from the ventral side; *b* abdomen of the same more highly magnified, and showing the adherent male; *Brl* oostegite; *K* branchial laminae (from Claus after Cornalia and Panceri).

in the genus *Cryptoniscus* in which, in the adult female, all crustacean characters are lost (Fig. 302).

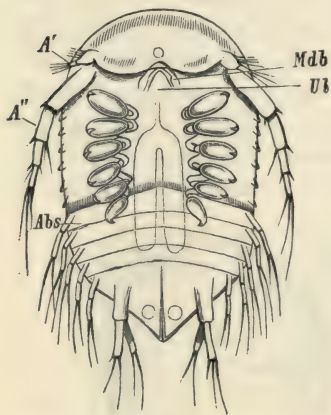


FIG. 300.—Larva of *Bopyrus virbii*, with six pairs of thoracic legs (after R. Walz). *A'*, *A'''* two pairs of antennae; *Abs* first abdominal segment; *Mdb* mandible; *Ul* under lip.

dwarfs (2–4 mm.) and are found clinging to the abdomen of the female (Fig. 299).

The Cryptoniscidae are parasitic on the bodies of the Cirripede group the Rhizocephala, which themselves in the course of a remarkable life history (p. 428) appear as externally projecting parasites on Decapod Crustacea.

It has been shown by Kossmann, Giard and Bonnier and by G. Smith that the individuals of the Cryptoniscidae are hermaphrodite and protandrous. In the young free-swimming state, in which they resemble the larvae of the Bopyridae, the paired testes are fully developed and the ovaries (Fig. 301) form small paired lobes, at their inner and anterior margins. In *Cryptoniscus* the larvae are some 1.14 mm. in length, and are provided with well-developed eyes having single lenses. In this male phase they fertilize individuals in the female phase which are attached to the bodies of their hosts. They then attach themselves to a host, by means of the anterior thoracic claws and undergo a metamorphosis within the larval skin. The testes degenerate and are absorbed by a number of large "phagocytic" cells (Smith), while the ovaries develop. On the bursting of the larval skin a grub-like creature emerges, .9 mm. in length, and provided with a single pair of short and stout limbs situated behind its

In the Bopyridae, examples of which are *Gyge branchialis* (Fig. 299) which inhabits the branchial chamber of the Anomuran *Gebia*, and *Bopyrus squillarum* which gives rise to the tumour-like swellings which often appear on one side of the cephalothorax in prawns, the larva escapes from the brood pouch as a minute creature, $\frac{1}{4}$ to $\frac{1}{5}$ mm. in length, and with its posterior antennae and abdominal appendages adapted for swimming (Fig. 300).

On reaching the branchial cavity of its host, which from its small size it is able to enter, it undergoes a metamorphosis. The females grow more or less unsymmetrically to a considerable size, their limbs become small, or are lost altogether on one side, and a spacious brood pouch is formed by the development of large imbricated oostegites. The males on the other hand are

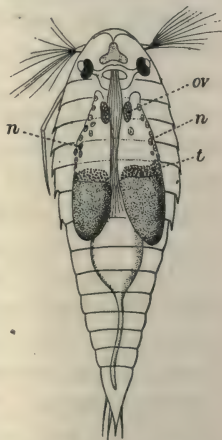


FIG. 301.—Dorsal aspect of the larva of *Danalia curvata*, in the male stage (after G. Smith). *n* phagocytic cells; *ov* rudimentary ovaries; *t* testes (from G. Smith).

mouth by means of which it buries its anterior portion, which becomes elongated, in the body of the Cirripede (Fig. 302) and thus absorbs the nourishment derived (in the case of the Rhizocephala) from the body of the crab or hermit crab on which in its turn the host is parasitic (Fig. 277, p. 430).

The dilated intestine ends blindly. The heart and ovary persist at the posterior end of the retort-shaped body, but the heart may disappear in the course of further growth. The eggs develop within the body of the mother, and escape by the bursting of the body wall.

The Entoniscidae go through a similar metamorphosis, the young in the male phase being attached to the bodies of the "females," as in the Bopyridae, but themselves afterwards passing into the female phase (*see* p. 491). A second form of male individual is, however, in the Entoniscidae, found on the "females," and these are regarded by Giard and Bonnier as "male" larvae which have for some reason failed to effect their further metamorphosis. So that we appear to have in this sub-family a case of sexual dimorphism in which as in some Cirripedes hermaphrodites and dwarf males occur, but here the phenomenon is complicated by the hermaphrodites being protandrous.

Section 1. ISOPODA GENUINA.

The second thoracic segment distinct from the cephalo-thorax, the eighth normally developed and bearing limbs. Seven thoracic limbs always present in the young, after the larval stage.

Tribe 1. ONISCOIDEA.

Woodlice. Body oval. First antennae vestigial. Mandibles without palps. Abdominal feet adapted for air breathing, the endopodites form delicate branchiae, the exopodites constituting horny opercula, which in the case of the two anterior feet in *Porcellio* and *Armadillium* contain air-chambers. Terrestrial.

Fam. 1. **Oniscidae.** *Ligia* Fab.; *Titanethes* Schiödte; *Ligidium* Brandt; *Styloniscus* Dana; *Trichoniscus* Brandt; *Philoscia* Latr.; *Deto* Guér; *Oniscus* Linn.; *Porcellio* Latr. (Fig. 297); *Cylisticus* Schnitzl.; *Platyarthus* Brandt; *Armadillidium* Brandt; *Pseudarmadillo* Sauss.; *Sphaeroniscus* Gerst.; *Periscyphis* Gerst.; *Armadillo* Latr.; *Tylos* Aud.; *Syspastus* Budde-Lund.

Tribe 2. ASELLOTA.

Some abdominal legs adapted for respiration in water and generally covered by the first, which form an opercular plate. Uropods terminal.

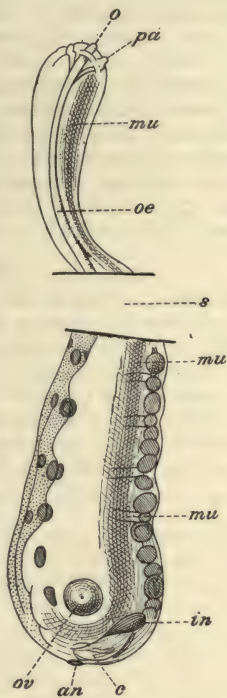


FIG. 302.—Young female of *Cryptoniscus paguri* (after Fraisse). *an* anus (impervious); *c* heart; *in* intestine; *mu* muscles; *o* mouth; *oe* oesophagus; *ov* ovary; *pa* papillae about the mouth; *s* skin of the Cirripede host.

Fam. 1. **Asellidae**. Body flattened, antennae with long flagella. All, or all but the first, abdominal segments fused and covered by a caudal shield. The two anterior pairs of abdominal feet small, the three next large and respiratory, the sixth styliform or lobed, and projecting posteriorly. Marine and fresh water. *Pleurogonium* Sars; *Leptaspidia* Sp. Bate; *Jaera* Leach; *Janira* Leach; *Asellus* Geoffr. (Fig. 295); *Munna* Kröy.; *Ischnosoma* Sars; *Paramunna* Sars; *Macrostylis* Sars.

Fam. 2. **Munnopsidae**. Eyes absent. Body elongated, often wide in the second in the fifth thoracic segments which bear elongated legs, and suddenly narrowed in the three posterior which bear lamellar swimming feet; abdomen unsegmented. Deep-water forms generally in high (N. and S.) latitudes. *Desmosoma* Sars; *Munnopsis* M. Sars; *Ilyarachna* Sars; *Eurycope* Sars; *Acanthocope* Beddard.

Tribe 3. PHREATOICIDEA.

Fam. 1. **Phreatoicidae**. Contains the two spp. of *Phreatoicus* described by Chilton,* *P. typicus* from a well in N. Zealand, and *P. australis* from 5,700 ft. on Mt. Kosciusko in the Australian Alps, and from Mt. Wellington in Tasmania. In the laterally compressed body, the disposition of the thoracic legs in two sets, the anterior curved backwards and the posterior forward, and other features, they present a remarkable resemblance to Amphipods. In the characters of mouth parts and pleopods they are however distinctly isopodan.

Tribe 4. VALVIFERA.

Elongated Isopods with paliless mandibles and abdominal terga fused to a caudal plate. The five anterior abdominal appendages are respiratory, covered by the valvular uropods, which are lateral.

Fam. 1. **Arcturidae**. 2nd antennae very long, the 2nd-5th thoracic legs setose, with minute terminal claws. *Arcturus* Latr. The 5th thoracic segment not much larger than the others. *Astacilla* Cordiner (*Leacia* Johnst.) 5th thoracic segment much elongated.

Fam. 2. **Idoteidae**. 2nd antennae not very long, strong claws on the anterior thoracic legs. *Chaetilia* Dana; *Edotia* Guér.; *Erichsonia* Dana; *Arcturides* Studer; *Cleantis* Dana; *Idotea* Fabr.; *Glyptonotus* Eights; *G. antarcticus* Eights, attains a length of 3½ inches and a breadth of 1¾ inches.

Tribe 5. FLABELLIFERA,

Uropods lateral, forming with the telson a terminal fin. The other abdominal limbs generally natatory.

Fam. 1. **Anthuridae**. Body linear, cylindrical, with short nearly equal antennae, and in some cases with piercing mouth-parts. One pair of maxillae absent. The anterior five pairs of abdominal feet respiratory, covered by a horny operculum—the exopodites of first pair; sixth pair enclosing the terminal abdominal segment between them. *Anthura* Leach, with paired otocysts in the telson; *Cyathura*, *Anthelura* and *Hyosura* Norm. and Stebbing; *Eisothistos* Haswell, *E. vermiformis* Haswell, in the tubes of the Serpulid *Vermilia*. *Haliophasma* Haswell; *Ptilanthura* Harger; *Paranthura* Sp. Bate; *Calathura* Norm. and Stebbing; *Cruregens* Chilton.

Fam. 2. **Sphaeromidae**. Body oval, highly arched, rolling more or

* C. Chilton, *Records of the Australian Museum*, vol. i. (1891), p. 149.

less completely into a ball. A posterior backward pointing dorsal spine is frequently present. *Limnoria* Leach, *L. lignorum* White, known at Plymouth as "the Gribble," gnaws out burrows in submerged wood-work; *Sphaeroma* Latr.; *Cymodoce* Leach; *Cerceis* M. Edw.; *Amphoroidea* M. Edw.; *Cassidina* M. Edw.; *Naesa* Leach; *Campecopea* Leach; *Ancinus* M. Edw.

Fam. 3. **Serolidæ**. Very broad and depressed Isopods, with the head sunk in the thorax. The second (and in the male the third) thoracic leg ends in a clasping foot, succeeding legs long and slender. The three posterior abdominal segments fused, three anterior abdominal appendages are setose swimming feet, the 4th and 5th respiratory, and the 6th narrow. *Serolis* Leach.

Fam. 4. **Aegidæ**. Body oval or elongated, not rolling into a ball; eyes usually large, first antennae usually conspicuously shorter than the 2nd. Both arise from the front margin of the head. The 2nd-4th thoracic legs short and directed forwards, the three posterior pairs do not end in hooks. Abdominal segments distinct. The 6th abdominal legs forming a fan-shaped swimming tail with the shield-shaped terminal segment of the body.

Sub-fam. 1. **Cirolanina**. With biting mouth parts. *Conilera*, *Eurydice* and *Cirolana* Leach; *Tachaea* Schiödte; *Corallana* Dana; *Barybrotus* Schiödte. Intermediate genus *Bathynomus* A. M. Edw. *B. giganteus* A. M. Edw. 9 in. long, at 955 fthms. between Cuba and Florida, also in Indian Ocean. Respiration carried on by means of branching processes of the endopodites of the abdominal appendages. Eyes very large, directed ventrally.

Sub-fam. 2. **Aegina**. With sucking mouth parts. *Aega* Leach. *A. spongiophila* Semper, inhabits the siliceous sponge *Euplectella*, in company with a species of *Palaemon*; *Rocinela* Leach; *Alitropus* M. Edw.

Sub-fam. 3. **Cymothoïna**. Shape of body as in other sub-families but antennae approximately equal, arising beneath front margin of head; mouth parts adapted for sucking; thoracic legs short and bear hooked claws; 5 anterior abdominal segments closely compressed and may be fused, 6th is large, shield-like, with broad swimming appendages. Parasitic on bodies of fish. *Aegathoa* Dana; *Olencira* Leach; *Ichthyoxenus* Herk; *Ourozeuktes* M. Edw.; *Harponyx* Sars; *Lobothorax* Bleeker; *Glossobius* Sch. and M. *G. linearis* Dana, infects the mouths of Flying Fish. *Livoneca* Leach; *Renocila* Miers; *Ceratothoa* Dana; *Nerocila* Leach; *Anilocra* Leach, *A. gigantea* attains 3½ in. length; *Cymothoa* Fab. (Fig. 298). Last three genera hermaphrodite, protandrous.

Tribe 6. EPICARIDEA.

Parasitic on other Crustacea. Females (or hermaphrodite individuals in the female phase, see below) degraded in structure and often unsymmetrical, males small and symmetrical. Abdominal limbs, if present, branchial and not covered by an operculum. Uropods terminal.

Fam. 1. **Microniscidæ**. On Copepods. *Microniscus* Fr. Müll. on *Calanus finmarchicus*, etc.

Fam. 2. **Cyproniscidæ**. On Ostracods. *Cyproniscus* Kossm. *C. cypridinae* (Sars) lives between the valves of the shell of *Cypridina*. Female reduced at last to a sack of eggs. Male, attached to female, also without appendages in adult state.

Fam. 3. **Dajidae.** On Schizopods. Adult female with only 5 pairs of thoracic legs, body curved round the eggs. Male completely or imperfectly segmented in adult state. *Dajus* Kröy. on *Mysis* and *Siriella*. *Aspidophryxus* Sars; *Notophryxus* Sars; *Heterophryxus* Sars.

Fam. 4. **Cabiropsidae.** On free or parasitic Isopods. Female, in adult state, reduced to an incubatory pouch folded round the brood. Embryo with peculiar ventral abdominal shield. *Clypoeniscus* G. and B.; *Munnoniscus* G. and B.; *Seroloniscus* G. and B.; *Cabirops* Kossm. on *Bopyrus*.

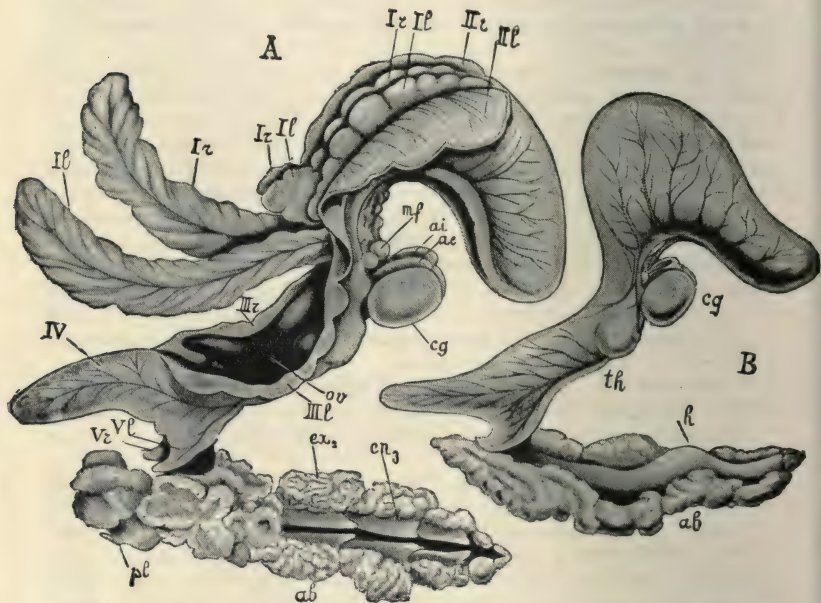


FIG. 303.—Adult female of an Entoniscid (*Portunion maenadis*) (from Lang's Textbook, after Giard and Bonnier). *A* with the brood cavity partly opened in the ventral median line and the brood lamellae separated; the ventral side of the abdomen is seen. *B* with the brood cavity intact, and the abdomen seen from the dorsal side. *I*r the anterior, middle and posterior lobes of the first brood lamella of the right side; *II* the same of the left side; *II*r and *l* second brood lamellae, right and left; *III*r and *l* third brood lamellae, right and left; *IV* fourth brood lamellae; *V*r and *l* fifth brood lamellae, right and left; *ab* abdomen; *ve* second, *ai* first antenna; *cg* cephalogaster (dorsal surface of head containing paired diverticula of the alimentary canal); *en*₃ endopodite of third abdominal appendage; *ex*₂ exopodite of the second abdominal appendage; *h* cardiac prominence; *mf* maxilliped; *ov* ovary; *pl* pleural lamella of first abdominal segment; *th* thorax.

Fam. 5. **Podasconidae.** On Amphipods of the sub-families Ampelisca and Lysianassina. Adult female reduced to an incubatory pouch, which is closed ventrally by the fused oostegites of the 5th thoracic legs. Male unknown. *Podascon* G. and B. on *Haploops*.

Fam. 6. **Cryptoniscidae.** Hermaphrodite and protandrous parasites on the Rhizocephala or other Cirripedes. Adult symmetrical; all or most of the appendages have disappeared. *Cryptoniscus* Fr. Müll. (Fig. 302), *Danalia* Giard (Fig. 301), *Liriopsis* M. Sch. (= *Liriope* Rathke). *Eumetor* Kossm. paras. on spp. of *Peltogaster* and *Sacculina* and their allies. *Cryptothir* Dana (?= *Hemioniscus* Buchholz) on non-parasitic Cirripedes.

C. balani (Bate) in the mouth space of *Balanus balanoides*; *Leponiscus* Giard, *L. pollicipedis*.

Fam. 7. **Entoniscidae**. The females (Fig. 303) when fully grown are markedly deformed, the abdomen being bent dorsally, 2-3 cm. in length, and enclosed within the bodies of *Brachyura* and *Anomura*, which they enter as larvae from the branchial cavity, the hypodermis of the host being invaginated and forming an envelope for the parasite. The aperture of invagination remains open as a respiratory passage. Brood lamellae large, lobed; thoracic feet vestigial; abdominal feet branchial. Two kinds of males with ripe testes, both very minute, are found about the female: one active 3 mm. long with well developed appendages; the other 1 mm. long somewhat degenerate and torpid. From the presence of vesicles containing spermatozoa on the last thoracic segment of the young female, and of the remains of testes (?), it is supposed, as in the case of the last family, that the animals are hermaphrodite and protandrous, being at first male, and subsequently acquiring the female form. The males of the second kind have, it is supposed, failed to effect this transformation and remain permanently male. *Entoniscus* Fr. Müll. on *Porcellana*; *Entione* Kossm. on *Achaeus*. *Grapsion* G. and B. on *Pachygrapsus*; *Cancrion* G. and B. and *Portunion* G. and B., spp. on various *Brachyura*. *P. maenadis* abundant on *Carcinus maenas* Penn. ("on 1 in 100").

Fam. 8. **Bopyridae**. Parasitic in the branchial cavity or elsewhere about the body of Decapod Crustacea. Sexual dimorphism very marked. Female large, flattened, usually unsymmetrical, blind and with vestigial antennae, mandibles styliform and other mouth parts much reduced. Thoracic feet (6-7) short and hooked, abdominal may be absent, or (*Ione* and its allies) long, branched and filiform. The dwarf males are symmetrical, long in proportion to their breadth (Fig. 299) and retain their eyes. *Phryxus* Rathke; *Athelgue* Hesse (= *Athelgus* and *Athelges*) on Pagurids; *Pleurocrypta* Hesse, on *Porcellana* and *Galathea*. *Palaegyge* G. and B. on Caridea, *Pseudione* Kossm. and *Gyge* Cornalia and *Panceri* on the *Anomura* (Fig. 299); *Kepon* (= *Cepon*) Duvernoy on a crab; *Leidya* Cornalia and *Panceri*, on *Gelasimus*; *Grapsicepon* G. and B.; *Cancricepon* G. and B. and *Ergyne* Risso (= *Portunicepon* Kossm.) on *Brachyura*; *Gigantione* Kossm.; *Ione* Lat. on *Thalassinidea*; *Argeia* Dana, *Bopyrus* Lat. (Fig. 300), *Probopyrus* G. and B., *Bopyrina* Kossm., *Bopyroides* Stimpson and *Hemiarthrus* G. and B. on Caridea. *Phyllodurus* Stimpson on *Upogebia*.

Section 2. ISOPODA ANOMALA.*

The second thoracic segment (the first free segment in other Isopods) fused with the head, the eighth reduced and without appendages. There are only five ambulatory limbs.

Fam. **Gnathiidae**. Aberrant Isopods which undergo a remarkable metamorphosis. The young, apparently until the last moult, though

* Dohrn, A., Unters. ü Bau und Entwick. der Arthropoda, 4. Entwick. und Organ. von *Praniza* (*Anceus*) *maxillaris*, *Zeits. f. wiss. Zool.* vol. 20 (1870), p. 53. See also Hesse, Mém sur les *Praniza* et les *Ancées*, *Ann. des Sc. Nat. Sér. 4*, 9 and *Sér. 5*, 19. Sp. Bate and Westwood, *Brit. Sessile-Eyed Crustacea*, and G. O. Sars, Crustacea of Norway, *Isopoda*, p. 50.

The Gnathiidae are included by Sars in the Tribe Flabellifera.

freely locomotive, live on the juices of other animals, the mouth parts being suctorial. The eyes are larger than in the adult and the mouth parts are all present and styliform and the upper lip forms a half-tube. The second thoracic legs, modified into a second pair of maxillipeds, lie parallel with the mouth parts and are strongly hooked. From such larvae the two sexes emerge, after the last moult, in very different forms. In the male (*Anceus* Risso, but *Gnathia* Leach has the priority) the head is very large and bears powerful prehensile mandibles, like those of a beetle, on its truncated front margin.* The maxillae have disappeared and the mouth is a small orifice in the middle of the concave under side of the head. The maxillipeds are broad, applied together as usual, and bear a setose 4-lobed palp. The second thoracic feet are wide and valvular and the segment to which they belong is small and closely united with the head, the 3rd and 4th segments distinct, the 5th-7th wide and more or less completely fused together. The 8th has disappeared.

In the female (which has been described as a distinct genus under the name *Praniza* Latr.) the head is much smaller though the eyes are larger than in the male. The mandibles are absent, and the middle of the body (4th-6th thoracic segments) is distended into a thin-walled sack. The brood pouch is formed between the hypodermis of the under part of the body and the cuticle which latter eventually splits segmentally allowing the larvae to escape. The mode of fertilization of the eggs, and of their entry into the brood pouch, have not been followed.

It appears that in the adult state food is brought to the mouth in currents, caused by the rhythmic movements of the maxillipeds.

The genus *Gnathia* Leach is marine, and most species are littoral. *G. maxillaris* Mont. in calcareous sponges; British. *G. Halidayi* young parasitic on fish, adults live independently in tubes (Delage). *Euneognathia* Stebbing was obtained by the *Challenger* from a depth of 900 fthms. in the N. Atlantic.

Order 6. AMPHIPODA.†

Malacostraca without a dorsal shield, with laterally compressed body and gills on the thoracic feet and (except in the Laemodipoda)

* Dohrn finds that these appendages are developed independently of the mandibles of the larva, and hence refuses to recognize them as mandibles.

† C. Spence Bate, *Catalogue of Amphipodous Crustacea in the British Museum*, London, 1862. E. van Beneden et Em. Bessels, *Mém. s. la form. du Blastoderme chez les Amphipodes, etc.*, Bruxelles, 1868. C. Claus, *Der Organismus der Phronimiden*, Arb. Zool. Inst. Wien, T. 2, 1879. Delage, V. *Contrib. à l'étude de l'appareil circulatoire des Crustacés edriophthalmes marins*, Arch. de Zool. exp., ix, 1881. O. Nebeski, *Beiträge zur Kenntniss der Amphipoden der Adria*, Arb. Zool. Inst. Wien, T. 3, 1881. Paul Mayer, *Fauna und Flora des Golfes von Neapel*, monog. VI. *Caprelliden*, Leipzig, 1882. Nachtrag, monog. XVIII., 1890. Id., *Die Caprellidae der Siboga-Expedition*, Leiden, 1902. C. Claus, *Die Platysceliden*, Wien, 1887. T. R. R. Stebbing, *Challenger Amphipoda*, 1888. G. O. Sars, *Hist. Nat. d. Crustacés d'eau douce de Norvège*. Christiania, 1867, and *An account of the Crustacea of Norway*,

with an elongated abdomen, the three anterior segments of which bear swimming feet, while the three posterior bear posteriorly directed feet adapted for springing (Fig. 304). The heart lies in the thorax, and the eyes are not faceted.

The Amphipoda are small animals, attaining only in rare cases a length of several inches. They move in the water principally by springing and by swimming. The "head" always includes the first thoracic segment, and, in the Laemodipoda, the second as well. It is sometimes small (*Gammarina*, Fig. 304), sometimes large and much swollen (*Hyperina*, Fig. 307), and is generally sharply distinct from the succeeding region.

The two pairs of antennae usually consist of a short strong shaft and a long



FIG. 304.—*Gammarus neglectus* (= *G. pulex*) (after G. O. Sars), with eggs between the brood lamellae (which are hidden by the coxopodites) on the thorax. *A'*, *A'''* the two antennae; *F*¹ to *F*⁷ the seven pairs of thoracic appendages; *Kf* maxilliped; *Sf* the first swimming foot of the abdomen.

multiarticulate flagellum, which however may be more or less rudimentary. The anterior antennae which are always longer and are frequently beset with olfactory hairs in the male, often bear a short accessory flagellum, a character not present in the Isopoda. In the *Hyperina* they are very short in the female, though of considerable length in the male (Fig. 307). The posterior antennae are always simple, and are frequently longer than the anterior; in the male of the *Hyperina* *Anomala* they are folded in a zig-zag fashion, and in the *Corophiidae* are strong and pediform. In the female of *Phronima* they are represented only by the basal joint (Fig. 307 a).

The mandibles are powerful biting plates with a sharp, usually toothed edge, a blunt masticating process, and, usually, a three-jointed palp. The bi-lobed anterior maxillae also have as a rule a short two-jointed palp (Fig. 305), while the maxillae of the second pair are reduced to two lamellae springing from a basal

Bd. 1, Amphipoda, Christiania, 1890-95. Della Valle, *Gammarini del Golfo di Napoli. Fauna and Flora Golf. Neapel*, Monographie 20. T. R. R. Stebbing, Amphipoda, 1. Gammaridae, *Das Thierreich*, Berlin, 1906. Compare also Bovallius and others.

joint. The *maxillipeds* * (first thoracic appendages) are in many cases seven-jointed (as are the succeeding appendages), but their basal segments are fused in the middle line, forming an under-

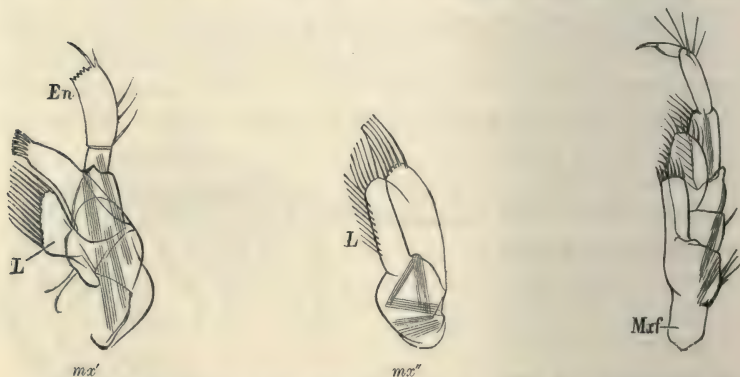


FIG. 305.—*Mx'* first maxilla; *mx'* second maxilla; *Mxf* maxilliped of *Gammarus* (from Claus); *En* endopodite; *L* basal endite.

lip, comparable with the labium of insects. The two succeeding segments of the maxillipeds bear lobes on their inner margins which project forward on the median side of the 4-jointed terminal part of the appendage which forms the palp. They are without an epipodial plate. In the *Hyperina* the maxillipeds are represented by a median plate (Fig. 306), bearing a pair of small setose lobes in front.



FIG. 306.—*Hyperia galba*. The maxillipeds (after Gerstaecker).

In the *Laemodipoda* the segment which in other *Amphipods* is the first free thoracic segment is fused with the head to form a cephalothorax.

The *legs* of the seven free *thoracic segments* are disposed in two groups, the four anterior having the terminal segments directed backwards and the three posterior having those segments directed forwards.

The basal segments (coxopodites) of the thoracic legs are in

* The following nomenclature is adopted by Stebbing, in his monograph on the *Gammaridae* (the *Gammarina* of this work) in *Das Tierreich*.

Thoracic appendage	1	— maxilliped
„ appendages	2 and 3	— gnathopods 1 and 2
„	4 to 8	— peraeopods 1 to 5
Abdominal	1 to 3	— pleopods 1 to 3
„	4 to 6	— uropods 1 to 3

the Gammarina and some Hyperina often expanded into wide lamellae* (Fig. 304) which may be suturally or movably united with the thorax. In some genera they are much reduced and in *Phronima* and its allies they do not exist as separate segments. The ends of some of the anterior limbs are frequently modified for prehension. In a few cases (Hyperina) a true *chela* is produced, the terminal or two terminal segments being opposable to a projecting process on the preceding segment (Figs. 307); but more usually the limb ends in a clasping "*hand*" in which the terminal segment folds back, like the blade of a pocket knife, on its predecessor. In either case the structure is often larger in the male. In the Caprellidae (Fig. 308) the number of legs is often reduced.

It is probable (as already stated, p. 439) that both the branchiae and oostegites are to be regarded as epipodial appendages of the thoracic limbs, and homologous with the two epipodia of the legs of *Anaspides*.

The **branchiae** are usually simple lobes attached near the bases of six or fewer of the posterior thoracic legs, and project on the inner sides of the limbs. They may be attached to the coxopodite of the limb or to the adjoining ventral surface of the segment of the body. On the view of their epipodial nature we should expect to find them attached to the outer surface of the limb, and in some forms at any rate (*Gammarus*) the branchial pedicle springs from the outer side of the posterior margin of the leg, although the plate curls round and lies internal to it. In some Lysianassina the structure of the branchiae is complicated by the development of secondary folds on one or both faces. In the Caprellidae, though some segments of the thorax are without limbs, the branchiae are nevertheless present on them.

The **oostegites** usually spring from the coxopodites, nearer the base than the branchiae, or from the adjoining surface of the thoracic segment, and curving inwards overlap one another across the middle line, forming the floor of the brood pouch. They are borne by from two to four pairs of legs, namely those belonging to the 4th and 5th, or to the 3rd to the 6th thoracic

* These coxopodites are often termed "epimerites" in works on amphipod anatomy, but as this word is used by some authors for the region of the body between the base of an appendage and the pleuron, and by others for the pleuron itself, it is clearly inconvenient to apply it to a part of the appendage.

segments. Like the branchiae, they may, in the Laemodipoda, be present on a segment which bears no other trace of an appendage.

Of the six *abdominal segments* of the Amphipoda Genuina the three anterior are large and bear the swimming feet, which consist of two multi-articulate and setose rami borne on a stout basal segment; the three posterior appendages are directed backward, and in the Gammarina form, with the terminal abdominal segments, the powerful organ with which, by the sudden extension of the abdomen, the characteristic leaps of these "sand-hoppers" are effected. The telson may be simple or (*Gammarus*) completely cleft.

In the Laemodipoda the abdomen is reduced to a short stump, with vestigial appendages (Fig. 308).

The **central nervous system** is present in the most simple condition in the Gammaridae in which the sub-oesophageal ganglion is succeeded by seven thoracic (one to each segment) and four abdominal ganglia, the three posterior segments being supplied by a single ganglion. In other groups the number of ganglia is reduced.

The **eyes** are compound, but do not project beyond the contour of the head.* The external cuticle forms a simple transparent covering and is not, as in Isopods, divided into lenticular corneal facets over the cones. In the Hyperina, which are pelagic, the eyes are very large, occupying the greater part of the surface of the head, and in one division of that group, the Phronimidae (Fig. 307) they are differentiated into dorsally directed and laterally directed parts. The retinal pigment is present, but that of the iris pigment cells is not developed in the Hyperina (Chun).

Otosacs have been described, by Claus, in the head of the pelagic *Oxycephalus*, in which they contain otoliths and lie in connexion with the dorsal surface of the brain, near the bases of the anterior antennae though not in them.

The *olfactory hairs* on the anterior antennae are referred to above. Small club-shaped structures borne by the posterior antennae, are known as *calceoli* and probably subserve some sensory function.

In the **alimentary canal**, the oesophagus leads into a *proven-*

* The sessile condition of the eyes in Amphipods and Isopods led to their classification in a group, the Edriophthalmata (—Arthrostraca), in opposition to the Podophthalmata, or stalk-eyed Crustacea.

triculus with a cuticular lining thickened into two paired sets of chitinous plates, and provided with lateral setose folds forming a straining apparatus. The *mid-gut* which succeeds, possesses a glandular dorsal diverticulum, and receives ventrally the paired orifices of the two or four "liver" tubes (much reduced in the Phronimidae). A pair of tubular glands, endodermal in origin, open at the posterior end of the mid-gut, in the Gammarina. Their supposed excretory nature is very doubtful, as they may be much reduced in size in that group and are not found in the other divisions of Amphipods. On the other hand the *antennary gland*, the equivalent of the green gland of Decapods is present, its coiled duct opening at the base of the second antenna.

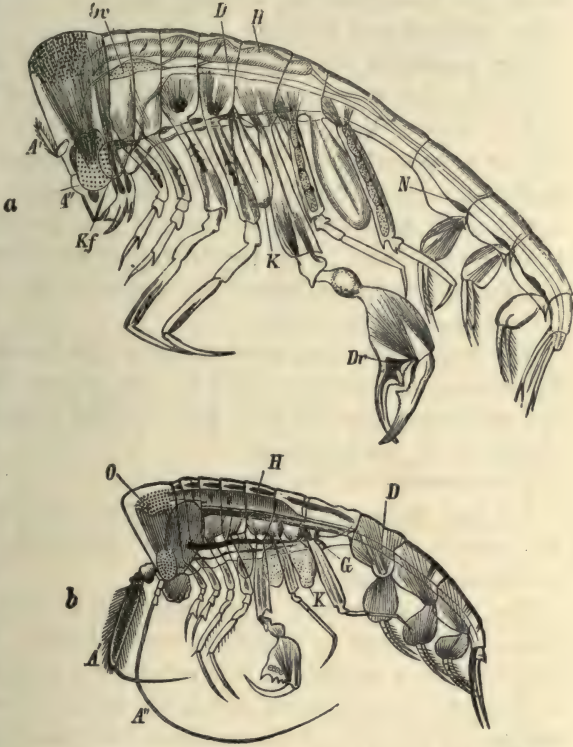


FIG. 307.—*Phronima sedentaria*. *a* female; *b* male; *A'*, *A''* first and second antennae; *D* intestine; *Dr* glands in the chela of the fifth leg; *G* genital orifice; *H* heart and aorta; *K* branchiae; *Kf* mandible; *N* nervous system; *O* eye (upper portion); *Or* ovary (after Claus).

In the Corophiidae groups of *unicellular glands* are present in the third and fourth thoracic appendages, on the terminal claws of which they open. Their secretion is used in constructing the tubular dwellings of this family.

The **heart** lies in the thorax in a pericardial sinus, with which it communicates by three (or fewer) pairs of lateral ostia; and

gives off arteries directed anteriorly and posteriorly. The *branchiae* are elongated and flattened sacs in relation with the bases of the thoracic limbs, as above described. The blood from them returns direct to the pericardial sinus where it mixes with venous blood from other parts of the body. In the species of *Orchestia* and *Talitrus* which live in moist situations on land, the *branchiae* are spirally twisted. In the Cyamidae they are long and tubular.

The **generative organs** are tubular and much alike in the two sexes, but the ducts of the male open, as usual, on the eighth, those of the female on the sixth thoracic segment. The former are situated on papillae, and abdominal feet are not modified, as in some Isopods, as copulatory organs. Nebeski has described a remarkable condition of the generative gland in the male *Orchestia*. The posterior part produces spermatozoa, but the anterior part consists of *primitive ova*, which however do not become functional.

The males are distinguished from the females not only by the absence of oostegites, but by the stronger development of the prehensile thoracic feet, and by the shape and sensory structures of the antennae.

The spermatozoa are filiform.

The eggs undergo their development in a brood pouch beneath the thorax of the female, being covered by the lamellar oostegites (2-4 pairs).

The yolk sometimes (*Gammarus locusta* and other marine species) undergoes a complete segmentation. Sometimes (*G. pulex*), after a superficial segmentation, a peripheral cell layer is formed, which secretes a delicate larval membrane beneath the egg membrane. A ventral primitive streak is then formed, and on the dorsal side a peculiar globular organ arises by invagination, with an orifice which has been erroneously taken for a micropyle. This is the first rudiment of a structure, known as the cervical gland (*dorsal organ*), which is confined to embryonic life. It is regarded by Grobben as homologous with the cervical gland of Branchiopods. The appendages are developed from before backwards, and the body of the embryo is ventrally flexed, the reverse of the position in Isopods. The young animals usually possess all their appendages at hatching, and in all essential external points have the structure of the

adult animal, though the number of segments of the antennae and the special form of the legs still present differences. In the Hyperina the just hatched young may be without abdominal feet and differ so much in their form from the adult that they may be said to undergo a metamorphosis.

The Amphipoda are inhabitants of all seas from the arctic and antarctic zones, in the former of which they are particularly abundant, to the equator. The Hyperina are pelagic, and lead a predatory existence among the pelagic fauna (cf. p. 502). Several species, borne about in ocean currents, have a very wide distribution.

The Gammarina are to a large extent littoral, but they also inhabit streams, and inland lakes. 116 species have been found in Lake Baikal, and they are represented in the lakes of Colorado, Switzerland and Scandinavia. Some species which live in the Arctic Ocean are also found in the fresh-water lakes of Norway and Sweden. *Niphargus*, and species of the allied *Crangonyx*, *Gammarus* and *Calliopius*, all wholly or partially blind, inhabit wells and subterranean fresh-water channels in different parts of the world. The Orchestiidae in general haunt the shore, peopling the lines of seaweed thrown up on beaches, and some occur in damp places on land.

The Caprellina are also littoral but occur also in the open ocean on floating seaweed. The Cyamina are parasitic on the skins of Cetacea.

The Corophiidae live in tubular galleries which they construct from surrounding materials, and *Chelura* in holes which it gnaws in wood, thereby damaging the submerged timbers of docks, etc.

The large size of the deep-sea forms is remarkable, *Lysianassa magellanica* attains 8 cm., a length which however is surpassed by the much attenuated Hyperid *Cystosoma Neptuni* (8.4 cm.) and the Oxycephalid *Rhabdosoma armatum* which reaches 12 cm. (nearly 5 inches).

Sub-order 1. AMPHIPODA GENUINA.*

Amphipoda with seven distinct thoracic segments. The

* The classification here adopted is based on that given by Gerstaecker in Bronn's *Klassen u. Ordnungen der Arthropoden*. For the classification of the Gammarina (Gammaridea) the reader should consult the description, which has recently appeared, by T. R. R. Stebbing in *Das Tierreich*. For the Caprellina (*Laemodipoda*) the works of P. Mayer should be consulted.

abdomen well developed, usually with seven segments, and with the three anterior feet differing in shape from the three posterior. Branchiae lamellar.

Division 1. GAMMARINA

Head and eyes small; antennae alike or nearly so in the two sexes; maxillipeds with multiarticulate pediform palps. The two anterior pairs of legs (belonging to the 2nd and 3rd thoracic segments) frequently end in prehensile claws, and in many cases the proximal segment in the four anterior, the two proximal segments in the three posterior pairs are widened to lamellae.

Tribe 1. COROPHIINA.

Body not compressed, half cylindrical; mandibular palp present, the basal joints of the thoracic legs short, antennae strongly developed.

Fam. 1. **Cheluridae**. Anterior antennae with an accessory flagellum, posterior with a setose lancet-shaped plate in place of a flagellum. The seven posterior thoracic segments all free, and approximately equal. The 4th–6th abdominal segments fused. The 3 last abdominal feet large and of peculiar shape. *Chelura* Phil. Bores in submerged timber, destroying dock-works. Europe and America.

Fam. 2. **Dulichidae**. Both antennae with strong, elongated shafts and short flagella. The seventh and eighth thoracic segments fused, and the 6th–8th thoracic legs very long, the two anterior pairs with a prehensile blade; 4th and 5th abdominal segments fused, and one of the terminal pairs of abdominal legs absent. *Dulichia* Kroyer; *Laetmatophilus* Bruz.; *Xenodoce* Boeck. all N. Sea; *Cyrtophium* Dana, Atlantic, etc.

Fam. 3. **Corophiidae**. Both antennae with elongated setose shafts. The segments of the thorax and abdomen all distinct. 4th and 5th thoracic legs with unicellular glands. The 3 terminal abdominal legs and sometimes the terminal body segment furnished with spines or hooks, by which the animals maintain their position in the tubular cases or passages which they construct. *Corophium* Latr. 2nd antennae very long; *Siphonocetes* Kröy.; *Cerapus* Say; *Dercythoë* Dana; *Unciola* Say; *Hela* Boeck; *Podocerus* Leach; *Gammaropsis* Lilljeb.; *Aora* Kröy.; *Xenocheira* Hasw.; *Stimpsonia* Sp. Bate; *Dryope*, Sp. Bate; *Cratippus* Sp. Bate; *Podoceroopsis* Boeck; *Amphithoë* Leach; *Synamphithoë* White; *Protomedeia* Kröy.; *Microprotopus* Norm.; *Gossea* Sp. Bate; *Goesia* Boeck; *Xenoclea* Boeck; *Haplocheira* Hasw.; *Amphithoides* Kossm.

Fam. 4. **Iceilidae**. Body broad and depressed. Head broad in front, with projecting eyes. *Iceilius* Dana; *Icridium* Grube; *Phlias* Guér.

Tribe 2. GAMMARINA GENUINA.

Body much arched, laterally compressed, though with rounded thoracic terga. Basal joints of the second to the fifth thoracic legs generally large, sometimes very large. Antennae small.

Fam. 6. **Gammaridae**. With the characters of the Tribe. (The branchiae are not spirally twisted in Subfamilies 1–5).

Sub-fam. 1. **Lysianassina**. Head small, depressed, truncated in front, or indented by the base of the anterior antenna. The shaft of this appendage is thickened and its two terminal segments very

short. It bears an accessory flagellum. Flagellum of posterior antennae of the male sometimes whip-like. Basal segments of the 2nd-5th thoracic limbs shield-shaped and imbricated, the second and third are feebly prehensile. Dwellers in mud.

(a) Cutting edge of mandible almost simple. *Lysianassa* M. Edw.; *Eurytenes* Lilljeb.; *Anonyx* Kröy.; *Opis* Kröy.; *Callisoma* Costa; *Acidostoma* Lilljeb.; *Cyphocaris* Boeck; *Egidia* Costa; *Glycera* Hasw.

(b) Cutting edge of the mandible toothed. *Stegocephalus* Kröy.; *Pontoporeia* Kröy.; *Bathyporeia* Lindstr.; *Amaryllis* and *Cyproidea* Hasw.

Sub-fam. 2. **Phoxina**. Head depressed, produced into a rostrum and overlapping the bases of the anterior antennae. Terminal segments of the shaft of anterior antennae not short. Basal segments of the 2nd to 5th thoracic legs large. Dwellers in mud.

(a) Anterior antennae with accessory flagellum. *Lepidactylis* Say; *Phoxus* Kröy.; *Urothoe* Dana; *Lilljeborgia* Sp. Bate; *Phaedra* Sp. Bate; *Tiron* Lilljeb.; *Bruzelia* Boeck.

(b) Anterior antennae without an accessory flagellum. *Westwoodilla* Sp. Bate; *Monoculodes* Stimps.; *Kroyera* Sp. Bate; *Amphilochus* Sp. Bate; *Gitana* Boeck; *Astyra* Boeck; *Graya* Sp. Bate; *Laphystius* Kröyer; *Oedicerus* Kröy.; *Oediceropsis* Lilljeb.; *Halicreion* Boeck; *Pleustes* Sp. Bate; *Iphimedia* Rathke; *Odius* Lilljeb.; *Acanthonotus* Owen; and (?) *Epimeria* Costa.

Sub-fam. 3. **Prostomatina**. Head produced into a prominent rounded rostrum. Anterior antenna short, with an accessory flagellum. Eyes very large, the mouth parts are styliform and together form a conical projecting mass. Basal segments of thoracic legs large. The 2nd pair terminate in a peculiarly shaped and powerful chela. Only one species, *Trischizostoma Raschi* Boeck, is known. It has been taken on the body of a dog-fish (*Spinax niger*) and is probably parasitic. Male unknown. North Sea.

Sub-fam. 4. **Ampeliscina**. Head elongated, depressed. Eyes much reduced. Antennae with long flagella, but the accessory flagellum is not present in the first. Basal joints of thoracic legs large, setose at the margin. 4th and 5th abdominal segments not distinct. *Ampelisca* Kröy.; *Haploops* Lilljeb.; *Byblis* Boeck.

Sub-fam. 5. **Gammarina**. Head high, truncated anteriorly. Eyes compound. Antennae slender, the first often with an accessory flagellum. Mandibular palp nearly always present. Abdominal segments distinct. The sixth pair of abdominal legs either with a single or a double terminal lamilla. *Photis*, Kröy.; *Leucothoe* Leach; *Stenothoe* Dana; *Aspidophoreia* Hasw.; *Peltocoxa* Catta; *Danaia* Sp. Bate; (?) *Callimerus* Stebbing; *Pherusa*, *Calliope*, and *Atylus* Leach; *Helleria* Norm.; *Dexamine* Leach, mandibles without palps; *Batea* Fr. Müll.; *Brandtia* Sp. Bate; *Pardalisca* Kröy.; *Nicippe* Bruz.; *Eusirus* Kröy.; *Isaea* M. Edw.; *Macleayia* and *Polycheria* Hasw.; *Melita* Leach, in some species one of the 3rd thoracic limbs terminates in a large chela, especially developed in the male (Fr. Müller); *Maera* Leach; *Crangonyx* and *Gammarella* Sp. Bate; *Niphargus* Schioedte, with rudimentary eyes, inhabits subterranean waters; *Gammarus* Fab.; *Pallasea* Sp. Bate; *Constantia* Dyb.; *Melphidippa* Boeck; *Amathia* Rathke; *Gammaracanthus* Sp. Bate; *Weyprechtia* Stuxberg; *Amathillopsis* Heller.

Sub-fam. 6. **Orchestiina**. Head large, cubical. First antennae simple and mandibles without palps. The branchiae of the 3-5th legs short and spirally twisted. The three last pairs of abdominal legs short and powerful, the 6th with a single terminal lamella. Terminal abdominal segment short and thick. *Talitrus* Latr.; *Orchestia* Leach; *Hyale* Rathke. They frequent sea-coasts and inland waters; some species of *Orchestia* are terrestrial.

Genera of doubtful position *Uristes* Dana; *Guerinia* Hope; and *Synopia* Dana

Division 2. **HYPERINA**.

Head large and usually rounded. The greater part of its surface is usually occupied by the very large eyes, which are more or less completely divided into frontal and lateral portions. Second antennae small or rudimentary in the females. Maxillipeds much reduced and fused to form a plate limiting the mouth cavity behind (Fig. 306). Thoracic legs differing from one another much in shape, with small basal segments. Pelagic.

Tribe 1. **HYPERINA ANOMALA**.

Both pairs of antennae lie in excavations on the under side of the head. In the male the first pair has a swollen shaft, clothed with hairs, and bears a rudimentary flagellum, the second is very thin and long and folded on itself in a zigzag. In the female the second is short and straight. Sixth and seventh thoracic feet with the second segment broad and lamellar. The eighth is small or rudimentary.

Fam. 1. **Typhidae**. Head swollen; upper lip convex; thorax broad, somewhat depressed; abdomen much narrower, short and capable of being folded in against the thorax; the lamellar plates of the 6th and 7th pairs of thoracic legs very large and covering the whole under surface of the thorax. *Eutyphus* Claus (*Platyscelus* Sp. Bate); *Hemityphus*, *Paratyphus*, *Tetrathyryus*, and *Amphithyryus* Claus.

Fam. 2. **Scelidae**. Head and thorax as in *Typhidae* but the mouth parts projecting as a beak, the mandibles being narrow and elongated. The abdomen longer. *Tanyscelus*, *Parascelus*, *Schizoscelus* and *Euscelus* Claus.

Fam. 3. **Pronoïdae**. Head rounded, arched; both antennae present in the female; maxillae strong; body elongated and slightly compressed; abdomen large; plates of 6th and 7th thoracic legs of moderate size; eighth¹ rudimentary. *Pronoë* Guér.; *Eupronoë* and *Parapronoë* Claus; *Phorcus* M. Edw.

Fam. 4. **Lycæidae**. Resembling *Hyperia* in shape of body. Second antennae generally absent in the female; maxillae feebly developed; a pair of "otosacs" above the brain; plates of sixth and seventh thoracic feet not much enlarged; eighth pair with full number of segments. *Thamyris* Sp. Bate; *Lycæa* Dana; *L. pulex* commensal in Salps. *Paralycaea*, *Pseudolycaea*, *Lycæopsis* and *Simorhynchus* Claus.

Fam. 5. **Oxycephalidae**. Body elongated, laterally compressed, head produced into a beak-like prominence; 2nd antenna absent in the female; two "otosacs" above the brain; 2nd and 3rd thoracic legs with chaelae in which the two terminal segments are opposed to a process on the ante-penultimate; the 6th and 7th have slender plates, and the eighth is complete; abdomen large. *Oxycephalus* M. Edw., and *Rhabdosoma* White. *R. armatum* from the Atlantic and Pacific, one of the longest Amphipods known, attains a length of 120 mm.

Tribe 2. **HYPERINA NORMALIA.**

Both antennae arise from the frontal surface of the head ; the posterior is not folded in the male, in the female it is often absent or vestigial. The sixth and seventh thoracic legs present various modifications in size and shape.

Fam. 1. **Phronimidae.** Head large, often produced downwards. Eyes divided into dorsal, "frontal" and lateral regions, the ommatidia of the former being greatly elongated ; they occupying the greater part of the head. Both antennae long in the male, each with a many-jointed flagellum ; the first is short and without flagellum in the female, and the 2nd vestigial. The liver tubes are rudimentary.

Sub-fam. 1. **Phrosininae.** Body short, compressed, the three hinder pairs of abdominal feet broad and fin-like. *Anchylomera* M. Edw. ; *Phrosina* Risso ; *Primno* Guér.

Sub-fam. 2. **Phroniminae.** Elongated, the last thoracic segment long. Three hinder abdominal feet narrow. *Phronima* Latr. *P. sedentaria* Forsk. (Fig. 307) is a widely distributed species. Perfectly transparent, except for the retinal pigment of the eyes (it is absent from the iris cells) and a few purple pigment cells on the limbs. Chun concludes that *Phronima* and its allies live, except in the breeding season, in the dark deeper regions (300–600 fms.) of the ocean. At that season the females approach the surface and take possession of the gelatinous test of a *Pyrosoma* or Salp, or the nectocalyx of a Siphonophoran, the protoplasmic portions of the owner being consumed by her. (*Phronima* is known as "Napolitano" by the fishermen of Messina.) The males arrive at the surface later, and the brood when it leaves the brood pouch is sheltered in the test. After the breeding season the males probably die, and the female and the young descend to deep water. *Phronimella*, *Phronimopsis* and *Paraphronima* Claus. (?) *Tryphana* Boeck.

Fam. 2. **Hyperiliidae.** Head large and rounded. Eyes large. Both antennae are present in both sexes. Liver tubes well developed. *Themisto* Guér. *T. arctica* Kröy. attains a length of 60 mm. It is found at the surface and in deep water of arctic seas. *Cyllopus* Dana ; *Cystosoma* Guér. *C. neptuni*, 84 mm. long, from the deep sea (1,090 fathoms) ; *Tyro* M. Edw. ; *Hyperia* Latr. ; *Daira* M. Edw. ; *Mimonectes* Bovallius ; *Lanceola* Say.

Fam. 3. **Vibilidae.** Head small, truncated in front. Eyes small. Both antennae present, the first the stouter. Shape of the body like that of a Gammarid. *Vibilia* M. Edw. *V. Jeangerardi* Luc. commensal in *Salpa democratica*, Mediterranean.

Sub-order 2. **LAEMODIPODA.**

The first and second thoracic segments are fused with the head to form a cephalo-thorax. Abdomen reduced to a stump-like process of the thorax. Second and third free thoracic segments with paired saccular branchiae, but usually without legs.

Fam. 1. **Caprellina** (Fig. 308). Grotesque Crustacea with long and very attenuated bodies ending abruptly with the stump-like abdomen, and

long legs. They are inhabitants of the littoral zone, frequenting tufts of hydroids, polyzoa and algae, among which they lurk motionless. They are often of brilliant colours, harmonizing with the colour of their environment. According to Paul Mayer *Caprella dentata* is bright green or nearly colourless, according as it lives among algae or hydroids. They progress with a looping movement, like a stick caterpillar, or swim by repeated rapid flexions of the body. The cephalothorax is small. Both pairs of the forward directed antennae are well developed and bear long flagella. The mouth parts do not depart markedly from the usual Amphipod type. The legs of the second thoracic segment, which is more or less closely united with the head, bear grasping hands, as do those of the third pair. The fourth and fifth pairs may be well developed, or vestigial or absent, while the three posterior pairs are long and directed backward, ending in long claws. Branchial sacs on the third and fourth, sometimes on the second thoracic segments. The abdomen is very short, and may be entirely unsegmented. Only 2-3 pairs of stump-like appendages are developed on it. *Proto* Leach; *Caprellina* Thöms.; *Protella* Dana; *Aegina* Kröy.; *Caprella* Lam.; *Podalirius* and *Cercops* Kröy.



FIG. 308.—*Caprella aequilibra* (from Claus, after Paul Mayer). *K* epipodial branchiae.

Fam. 2. **Cyamina.** "Whale lice." They live attached by their powerful hind legs to the skin of Cetacea, and gnaw out pits in which they lie. Body broad and flat and compressed longitudinally. First antennae directed forwards, with long shaft and short flagellum, the second may be much reduced, four jointed. The mandibles without palps, first maxillae with a short unjointed palp, the second maxillae fused at their bases. Maxillipeds with a single inner lobe and a well developed or rudimentary palp. Second thoracic legs may be slender, the 3rd are powerful, 4th and 5th absent, 6th-8th with powerful hooked claws. The 4th and 5th segments bear the long branchial tubes. The wartlike abdomen is unsegmented, and bears the vestige of a pair of appendages. *Cyamus* Latr.; *Platycyamus* Lützk.

Order 7. STOMATOPODA.*

Elongated Malacostraca with short cephalo-thoracic shield which does not cover all the thoracic segments. The five anterior pairs of

* Besides Dana, M. Edwards and others, compare O. Fr. Müller, Bruchstück aus der Entwicklungsgeschichte der Maulfüsser, i and ii, *Arch. f. Naturgesch.*, xxviii, 1862, and xxix, 1863. C. Claus, Die Metamorphose der Squilliden, *Abh. Göttinger Soc.*, 1872. C. Grobben, Die Geschlechtsorgane von *Squilla mantis*, *Sitzungsber. der k. Akad. der Wissensch.*, Wien, 1876. W. K. Brooks, *Challenger Report*, Stomatopoda, 1886. H. J. Hansen,

thoracic feet are turned forwards as maxillipeds, the three posterior separate from them and biramous. The swimming feet on the strongly developed abdomen bear branchial tufts, and the sixth pair forms, with the telson, a caudal fin.

The Stomatopoda are a small number of closely related species inhabiting in the adult state coral reefs and sandy shores in the tropical and temperate regions of the globe. Though sharply separated from other Malacostraca, they present features of resemblance with the Amphipoda, Isopoda and Cumacea on the one hand and with the Decapods on the other.

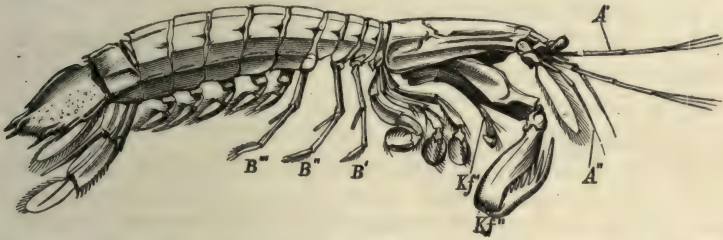


FIG. 309.—*Squilla mantis* (after Claus). *A'*, *A''* first and second antennae; *B'*–*B'''* the 6th–8th thoracic legs (biramous); *Kf'*, *Kf''* first and second maxillipeds.

The integument is thin and flexible. The five anterior segments of the thorax are crowded together behind the elongated cephalic region, and the dorsal shield is almost entirely a cephalic structure though overlapping the anterior segments of the thorax. It is less extensive in the adult than in the larva. The appendages of the five anterior thoracic segments are directed forwards about the mouth, and thus have the character of maxillipeds. Those of the three posterior thoracic segments are directed downwards. In the division of the thoracic legs into these two groups the Stomatopods resemble the Amphipods (Fig. 309).

The abdomen is large and powerful, and lodges several of the organs which in other Malacostraca are situated in the thorax.

The anterior region of the body is distinct from the dorsal shield and divided into two small movable segments, the anterior carrying the stalked eyes, the posterior the first antennae. The latter terminate in a flagellar endopodite and

Isopoden, Cumaceen and Stomatopoden, *Erg. der Plankton-Expedition*, Kiel, 1895. Orlandi S. Sulla struttura del intestino del *Squilla mantis*, *Atti Soc. Ligustica*, xii (1901), 2, p. 112.

an accessory flagellum which divides again (as in some Caridea) into two flagella, of which the outer is somewhat flattened, and beset with olfactory hairs. A movable plate, recalling that of *Nebalia*, projects from the front of the dorsal shield over this segmented region of the head.

The question arises—Is the segmentation of the front of the Stomatopod body the remains of a primitive segmentation, or is it secondarily acquired? The absence of a corresponding segmentation from the preoral part of the body of the entomostracan groups points to the latter conclusion.

The posterior antenna (A'') is biramous, the endopodite ending in a flagellum, and the exopodite consisting of a large oval scale.

The preoral region is considerably elongated. The anterior and posterior lips are well developed, and the *mandibles*, lying between them, bear a slender palp. The second pair of *maxillae* have a peculiar shape, with a lobed inner and outer border as in larval Penaeidea.

The region of the body to which the five maxillipeds are attached presents three tergal sclerites, which correspond to the three posterior appendages. In front of the anterior sclerite a membranous tract uniting it with the base of the dorsal shield, lies dorsal and anterior to the insertion of the great second maxillipeds. Hence it does not appear that more than the first thoracic segment is represented with the head region in the shield of the adult. In the larva the shield is entirely cephalic.

The *maxillipeds* are armed with prehensile claws, so shaped that the pointed terminal joint folds, like the blade of a pocket-knife, on its predecessor, and the limbs are so disposed that these joints are directed forwards and not backwards, as in Amphipods. The second pair, which are by far the largest, are the chief weapons of these exceedingly pugnacious animals. Each maxilliped bears on the outer side of its basal joint a stalked discoidal branchial lamella (epipodite). The three succeeding appendages ($B'-B'''$) are biramous and bear short styloform multiarticulate rami on their third segments, and their flattened terminal surfaces are thickly clothed with setae, like a hare's foot. According to Claus the shorter rami are the endopodites and the longer exopodites, and the stem of the appendage is two-jointed in the larva.

The gills on the large *swimming feet* of the *abdomen* consist of unbranched filaments disposed in transverse rows along the branches of an axis, which is inserted on the inner margin of the base of the exopodite. The uropods are without gills and, directed backwards, form with the distinctly jointed telson a powerful caudal fin.

In the **central nervous system** the supraoesophageal ganglion is a hexagonal mass (notwithstanding the apparent segmentation of the front of the body) supplying nerves to the eyes and both pairs of antennae. A compound ganglionic mass behind the oesophagus supplies the segments from the mandibular as far as the fifth thoracic, but the nine segments behind this have each their own ganglion. The compound **eyes** have the same structure as in Decapods. In *Squilla* the surface is not simply convex, but saddle-shaped. No auditory organ has been discovered.

In the **alimentary canal** the triturating stomach is only slightly developed. The intestine is a slender and delicate tube, 1 mm. in diameter in *Squilla mantis*, extending to the end of the fourth abdominal segment, where it joins the wider hind-gut. Parallel with the gut are two longitudinal canals, which open anteriorly by a common opening into the pyloric region of the stomach. Voluminous caecal diverticula are given off from these canals, which are segmentally disposed, in each posterior segment and in the telson, and almost completely envelop the intestine (Orlandi).

The glands of which these longitudinal canals are the ducts are evidently homologous with the "hepatic" digestive glands of other Crustacea. Before Orlandi's researches were published the segmentally arranged groups of caeca were supposed to open direct into the gut in Stomatopods and thus to present a puzzling exception to the usual arrangement.

Antennal glands are absent, but the presence of well developed **shell-glands** has been demonstrated by Kowalewsky.* An *excretory* function has also been suggested for a pair of rectal glands.

The **heart** is tubular with numerous paired *ostia*, and extends from the fifth abdominal segment to the front of the thorax, where it presents a small enlargement. Fourteen paired arteries are given off from it.

The **testes** are abdominal and take their origin in a slender median tube. The vasa deferentia open on the tips of the rod-like penes which spring from the basal segments of the last thoracic legs. A pair of "accessory glands" pass backward through the thorax to orifices situated close beside those of the vasa deferentia. The spermatozoa are spherical, with large nuclei. The males possess small processes of peculiar shape and

* A. Kowalewsky, Ein Beitrag zur Kenntniss der Excretionsorgane *Biol. Centralblatt*, Bd. ix (1889), p. 41.

obscure function, on the inner margins of the first pair of abdominal feet.

The ovary extends throughout the thorax and abdomen and like the testis is unpaired behind and paired in front. The oviducts converge to closely approximated openings in a median depression on the 5th thoracic segment, a small receptaculum seminis being situated between the orifices. On the sterna of the three following segments are *cement glands*.

Development. Our information on the earliest stages of the development of Stomatopods is imperfect. The eggs are small (.6 mm. in one species), but the form in which the young larvae are hatched is, in several genera, unknown. In some species at any rate the eggs are deposited by the mother in a

burrow, and are there aerated by currents of water produced by her respiratory movements.

The larvae are elegant, transparent creatures which lead a pelagic existence and undergo a marked metamorphosis. Before their rela-

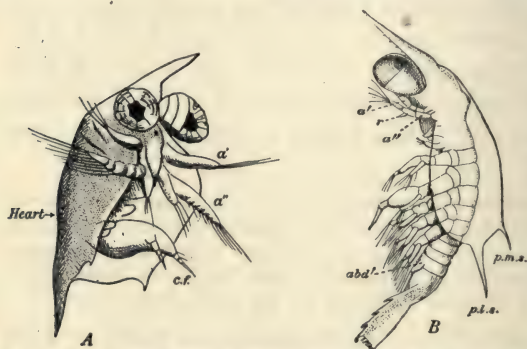


FIG. 310.—A Metanauplius larva regarded as the predecessor of the Erichthoidina stages (after Lister). B The youngest known Erichthoidina larva (after Hansen). *a'*, *a''* first and second antennae; *abd.* first abdominal legs; *c.f.* caudal fork; *p.l.s.* and *p.m.s.* postero-lateral and postero-median spines; *r* (in B) rostrum.

tion to adult Stomatopods was recognized they received generic names, two of which, *Erichthus* and *Alima*, have been retained to distinguish two somewhat different types.

The earliest (*Erichthoidina*) stage of the *Erichthus* type, whose connexion with succeeding stages has been traced, is comparable though not closely with the Protozoa stages of other forms (Fig. 311 A). A large cephalic shield, folded over at the sides, is produced into anterior and posterior median and into postero-lateral spines. The larva possesses a median and two well developed lateral eyes and five biramous swimming thoracic appendages of which the second is as yet only slightly the largest. Though all the thoracic segments are formed the three posterior

are as yet, and remain through several ecdyses, without limbs. The first abdominal appendages however appear at this stage, and a large caudal plate, the telson, terminates the body.

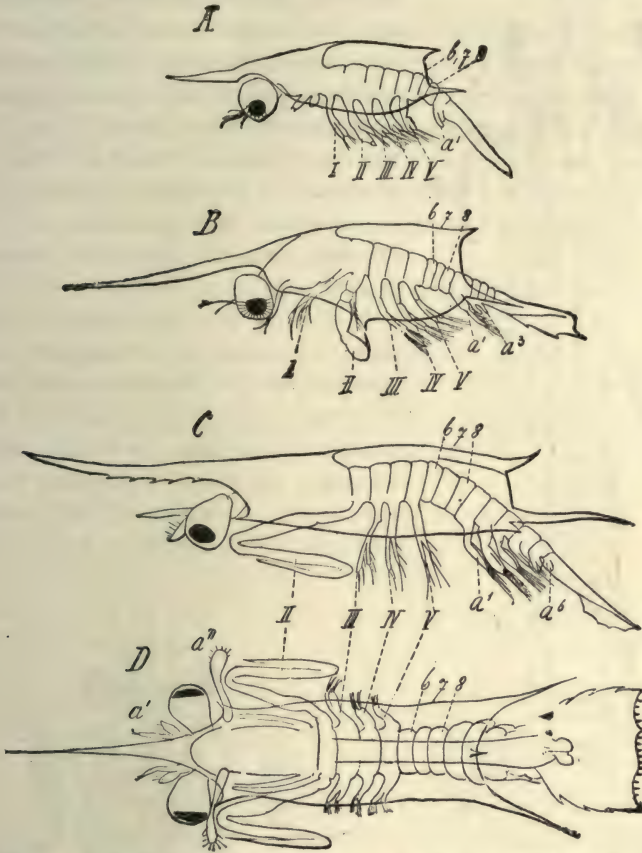


FIG. 311.—Four consecutive Erichthoidina stages. a' , a'' first and second antennae; a^1 – a^6 the six abdominal legs; I–V the five maxillipeds; 6, 7 and 8 the posterior thoracic segments, limbless at this stage (from Korschelt and Heider, after Claus).

It appears probable that the metanauplius represented in Fig. 310 A, is a Stomatopod larva in a still earlier stage than the Erichthoidina.* The fully formed condition of the eyes at this early stage, the large size and shape of the carapace, its limitation to the cephalic region and the disposition of its spines are features which connect it with the Erichthoidina. On the other hand the jointed caudal fork recalls the Phyllopod *Apus*. Its jointed character is a feature retained by no other known Malacostracan larva.

* Cf. J. J. Lister, On a (?) Stomatopod Metanauplius Larva, *Q.J.M.S.*, xli (1898), p. 433.

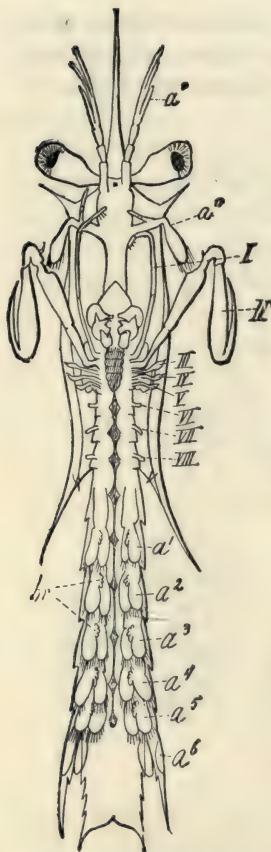


FIG 312.—Older *Erichthus* larva (from Korschelt and Heider, after Claus). *a'*, *a''* first and second antennae; *I-V* maxillipeds; *VI-VIII* rudiments of the posterior thoracic legs; *a1-a6* pleopoda; *br* branchial rudiments.

posterior thoracic legs are entirely absent (Fig. 313).

The stage in the life-history of Stomatopods in which the first and second thoracic limbs are well developed while the remaining thoracic limbs are reduced (*Erichthus*)

At what is known as the *Erichthus* stage of this larva (Fig. 312), which follows the *Erichthoidina*, all the abdominal appendages are developed and the two anterior pairs of thoracic legs are much elongated. The three succeeding legs have dwindled to an almost vestigial condition, and it is not until the later period of larval life that they elongate and acquire their chelate extremities. The rudiments of the 6th-8th thoracic legs have now appeared.

In *Squilla* the eggs hatch as *Alima* larvae at a stage of development corresponding to the *Erichthus* stage above described. The body is however more slender in proportion to the size of the carapace, the shape of the latter and of the telson is different, the cephalic region is much elongated, and the six

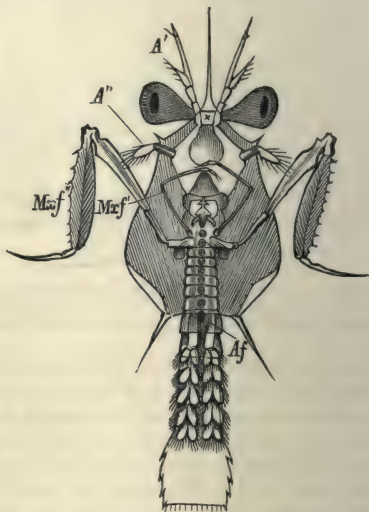


FIG. 313.—Young *Alima* larva (from Claus). *Af* abdominal feet (pleopods); *Mxf''* anterior maxillipeds; *Mxf'* the large maxillipeds (second pair).

or absent (Alima) may be compared with the zoea stage of Euphausiidae and the Decapods. It differs however from the zoea stage of these forms in that the abdominal legs are already developed.

Owing to the pelagic habit and the prolonged period of metamorphosis of the larvae, during which they are borne about by the perpetually circulating ocean currents, the species are widely distributed over the shores of temperate and tropical regions. The adults vary considerably in size from 38 mm. (*Chloridella microphthalma*) to 34 cm. (*Coronis maculata*). Some are of a uniform green colour, others are boldly marked with transverse stripes of yellow and brown.

Fossil Stomatopods have been found in the Jurassic and later formations.

Fam. **Squillina**. *Squilla* Fab. *S. mantis* Rondelet and *S. desmarestii* Risso have been taken on our shores. *Lysiosquilla* Dana; *Pseudosquilla* Dana; *Gonodactylus* and *Coronis* Lat.; *Odontodactylus* Bigelow; *Coronida* and *Protosquilla* Brooks, rostral spine of the larva retained in adult; *Leptosquilla* and *Choridella* Miers; *Pterygosquilla* Hilgdf.

Order 8. DECAPODA.*

Malacostraca in which all the thoracic segments, or all but the last one or two, are united with the head by the dorsal shield. The

* Herbst, *Versuch einer Naturgeschichte der Krabben und Krebse*, 3 Bde., Berlin, 1782-1804. Leach, *Malacostraca podophthalma Britanniae*, London, 1817 to 1821. Th. Bell, *A history of the British stalk-eyed Crustacea*, London, 1853. H. Rathke, *Untersuchungen über die Bildung und Entwicklung des Flusskrebsses*, Leipzig, 1829. Spence Bate, On the development of Decapod Crustacea, *Phil. Trans.*, London, 1859. Report on the Crustacea Macrura, *Challenger Report*, 24 (1888). C. Claus, Zur Kenntniss der Malacostrakenlarven, *Würzb. naturwiss. Zeitschr.*, ii., 1861. Fr. Müller, Die Verwandlung der Garneelen, *Archiv für Naturgesch.*, xix, 1863. Fr. Müller, Für Darwin, Leipzig, 1864. V. Hensen, *Studien über das Gehörorgan der Dekapoden*, Leipzig, 1863. C. Heller, *Die Crustaceen des Südlichen Europa*, Wien, 1863. P. Mayer, Zur Entwick. der Dekapoden, *Jen. Zeits.* Bd. xi (1877). C. Grobben, Beitr. z. Kenntniss d. männlich. Geschlechtsorgane der Dekapoden, etc., *Arb. Zool. Inst. Wien*, i (1878). J. E. V. Boas, Studier over Dekapodernes Slaegtskabsforhold, *Vidensk. Selsk. Skr.*, Kjöbenhavn, 1880. T. H. Huxley, *The Crayfish*, London, 1880. W. K. Brooks, Lucifer, *Phil. Trans.* 1882. H. Reichenbach, Studien zur Entwick. des Flusskrebsses, *Abh. Senckenberg. Nat. Ges. Frankfurt*, 1886. H. C. Bumpus, The Embryology of the American Lobster, *Journ. Morph.* v, 1891. E. Bouvier, Rech. Anat. s. l. syst. artérielle d. Crustacés Décapodes, *Ann. Sc. Nat.* 1891. W. K. Brooks and F. H. Herrick, The Embryology and Metamorphosis of the Macroura, *Mem. Nation. Acad. Science*, Washington, 1891. P. Marchal Rech. Anat. et physiol. sur l'appareil

eyes are stalked and compound. The first, second and third thoracic appendages are modified as maxillipeds, leaving five pairs of trunk legs, and there may be as many as four epipodial branchial rudiments corresponding to each of the thoracic legs.

The **cephalo-thoracic shield** or carapace attains its fullest development among the Decapods, involving in many cases all the thoracic segments, though in some groups the last segment (*Astacus*) in others the two posterior (*Brachyura*) remain free. The side of the carapace is formed by the pleural fold or branchiostegite, which ends in a free margin over the bases of the limbs and shelters the gills which lie between it and the body wall.

In the *Macrura Natantia* and *Reptantia* the cephalo-thorax is of an oval shape, ending in front in a pointed rostrum, the branchial cavities are lateral, and the abdomen is well developed, being as long as or longer than the carapace, and ends in a telson, which with the terminal appendages forms a powerful caudal fin.

In the *Brachyura*, on the other hand, the carapace is generally broader than it is long, the thoracic limbs are set wide apart, and the short abdomen does not end in a caudal fin but is bent forward and applied to the faces of the broad thoracic sterna (Fig. 316). Owing to the great expansion of the cephalo-thorax the branchial cavities lie rather beneath than at the sides of the thorax and the branchiostegite, especially in the anterior region, projects inwards forming the floor of the cavity (Fig. 316).

In the *Anomura* we meet with a variety of stages intermediate between the *Macrura* and the *Brachyura*, in these respects.

In the larger Decapods the skeleton is firmly calcified.

The so-called "cervical groove" of *Astacus* and many of the larger *Macrura* is regarded by Huxley,* and some later writers, as the limit

excréteur d. Crustacés Decapodes, *Arch. Zool. exp.*, 1892. A. Ortmann, Das Syst. d. Dekapodenkrebse, *Zool. Jahrb.* ix, 1897. See also Bronn's *Theirreich*, Crustacea Malacostraca, Leipzig. T. R. R. Stebbing, *A History of the Crustacea*. London, 1893 (Int. Scientific Series). A. Alcock, Materials for a Carcinological Fauna of India, *Journ. Asiat. Soc. Bengal*, Calcutta, 1895-1900. Id. *Desc. Catalogue of Indian Deep-Sea Crustacea Decapoda and Anomala in the Indian Museum*, Calcutta, 4to, 1901. W. T. Calman, On the Classification of the Crustacea Malacostraca, *Ann. and Mag. of N. H.*, Ser. 7, vol. xiii, 1904. N. K. Koltzoff, Studien üb. d. Gestalt d. Zelle. I. Unters. üb. d. Spermien d. Decapoden, *Arch. f. mik. Anat.* Bd. lxxvii (1906), p. 364. L. A. Borradaile, On the Classification of the Decapod Crustaceans, *Ann. and Mag. of N. H.*, Ser. 7, vol. xix (1907), p. 457. Id. Articles on Crustacea in J. S. Gardiner's *Fauna and Geography of the Maldives and Laccadive Archipelagoes*, Cambridge.

* *Crayfish*, p. 19.

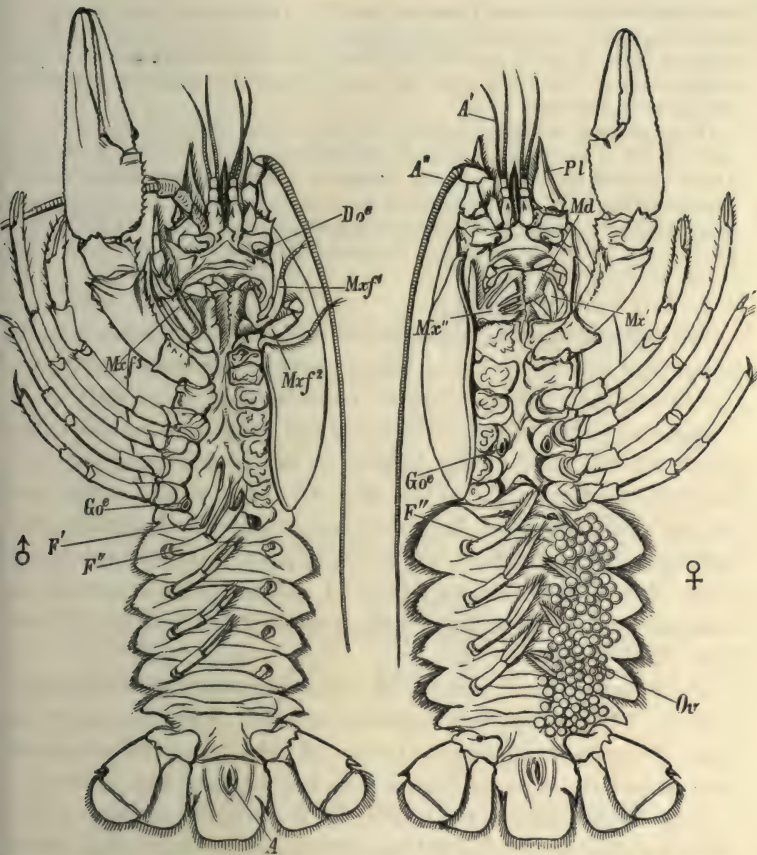


FIG. 314.—Male and female of *Astacus fluviatilis* seen from the ventral side. In the male the ambulatory and abdominal feet of the left side; in the female the ambulatory feet of the right side and the maxillipeds of both sides have been removed. *A* anus; *A'* antennules; *A''* antennae; *Do*° opening of the green gland; *F'*, *F''* first and second abdominal foot; *Goe* genital opening; *Md* mandible with palp; *Mx'*, *Mx''* first and second maxillae; *Mxf*¹ to *Mxf*³ the first three pairs of maxillipeds; *Ov* eggs; *Pl* scale of antenna. (After Claus.)

between the head and thorax. That this is the case appears very doubtful from a consideration of *Gnathophausia*. In this Schizopod, the dorsal shield extends back over the succeeding segments, but does not apparently fuse with them, the eight thoracic terga remaining distinct.* The shield appears to be in this case as clearly limited to the head region as that of *Apus* or *Nebalia*. Towards the front of the upper surface of the shield there is however a groove, which is identical in position with the "cervical groove" of *Astacus*. In *Gnathophausia* therefore it appears that the groove is very far from marking the posterior limit of the head.

It was named cervical groove by H. Milne-Edwards who regarded it as

* Cf. Sars *Challenger Report*, Schizopoda, pl. 8, Fig. 17.

the posterior limit not of the head but of the regions corresponding to the antennary and mandibular appendages, but the great variation in its position even in allied genera, its incompleteness in some forms, and its entire absence from many of the lower Decapods, render its segmental nature very doubtful.

Other grooves are often present on the decapod carapace, but as in the case of the cervical groove their morphological significance is obscure. These are well marked and may present a complex arrangement* in the Thalassinidea. Among them may be mentioned a pair of open longitudinal sutures dividing the median from the lateral regions of the cephalothorax, and known as the *lineae thalassinicae*. They are present in 3 out of the 4 families.

The projecting margin, or **pleural fold** of the carapace, is found in varying relations with adjacent parts in the several groups of the Decapoda. These must be considered in some detail.

Posteriorly the pleural fold forms the outer or lower boundary of the gill chamber and is known as the branchiostegite. Anteriorly it abuts against the sides of the oral apparatus, and in the Brachyura and Anomura, where the mouth regions have undergone specialization, the anterior part of the pleural fold of either side is separated by a *pleural suture* from the rest of the carapace and is known as the *pterygostomial* region (Figs. 315 and 316, *Pt.s*).

In the lower Macrura the sides of the carapace are little differentiated. The pleural fold extends forward to the region of the eyes, where it is excavated to allow of the play of the eye stalks, and anteriorly it is continued into the base of the rostrum.

The modifications to which it is subject in the higher Decapods are associated with modifications of the sternal region of the body in front of the mouth, known as the *epistome* (cf. Figs. 315 and 316). This area is bounded behind by the insertions of the mandibles and the base of the upper lip or *labrum*; the side limits are set by the pleural margins of the carapace and the anterior by the bases of the first and second antennae. In front, between the bases of the first antennae, the epistome often ends in a more or less prominent point in the middle line (Fig. 316). In the Caridea the epistome is of small antero-posterior extent, but in the Macrura Reptantia the length in this direction is considerably greater. In the Nephropsidae its pleural boundaries though clearly marked are low. In the

* Cf. Borradaile, Marine Crustaceans, Pt. xi. Gardiner's *Fauna and Geography of the Maldivé and Laccadive Archipelagoes*, vol. ii, p. 690.

Eryonidae and Scyllaridae there is no pleural fold at this part to separate the epistome from the sides of the carapace.

In the large group of the Anomura the pterygostomial region is separated from the carapace by a distinct and flexible suture (*s*) and forms a movable flap, which anteriorly projects freely at the sides of the epistome (Fig. 315). In the notch between this and the forward continuation of the pleural fold is set the second antenna. This is the relationship of the parts characteristic of the Anomura.

In the Brachyura the anterior part of the epistome is differentiated from the deeply excavated posterior part, and bears the first and second antennae on its front

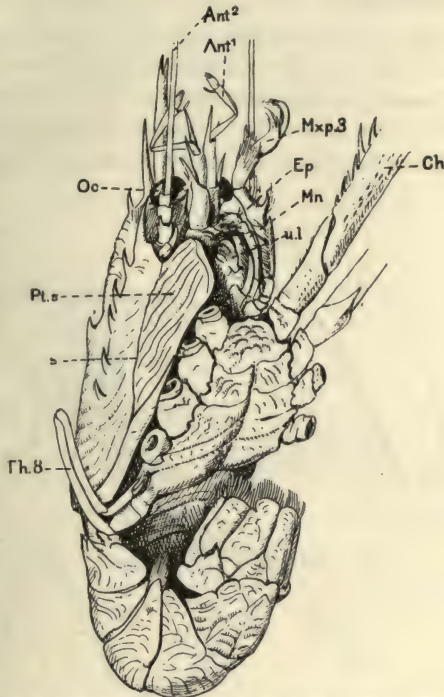


FIG. 315.—*Munida* showing the relations of the pterygostomial region to the epistome in the Anomura. *ant*¹ first antenna; *ant*² second antenna; *Ch* chelipeds; *Ep* epistome; *Mn* cutting edge of the mandible; *Mxp*³ pediform third maxilliped; *Oc* eye; *Pt.s* pterygostomial flap; *s* pleural suture by which it articulates with the carapace; *Th.8* slender last thoracic legs; *ul* upper lip

border. The pterygostomial region, although marked off in the Brachyura, from the rest of the carapace by the pleural suture, is not movable on it.* Anteriorly it abuts against the sides of the front part of the epistome, and, instead of projecting freely, joins with the latter by a suture (Fig. 316). This suture is most marked in the lowest group of the Brachyura, the Dromiidae. The ridge forming its outer border may be regarded as the pleural margin of the carapace.

* Its free margin forms the side of what is known as the *buccal frame*, limiting the recess in which the mouth parts are contained. This recess is closed by the door-like third maxillipeds (Fig. 316).

Anteriorly it becomes more prominent, and abuts against the base of the 2nd antenna, partially or completely limiting its movement. In most Brachyura the orbit is extended as a hollow in the side of the carapace, and the forward continuation of the pleural margin is to be sought in the floor of the orbit, near the base of the eye stalk. In the Oxyrhyncha the base of the 2nd antenna, epistome and side of carapace are fused together, all trace of sutures being obliterated.

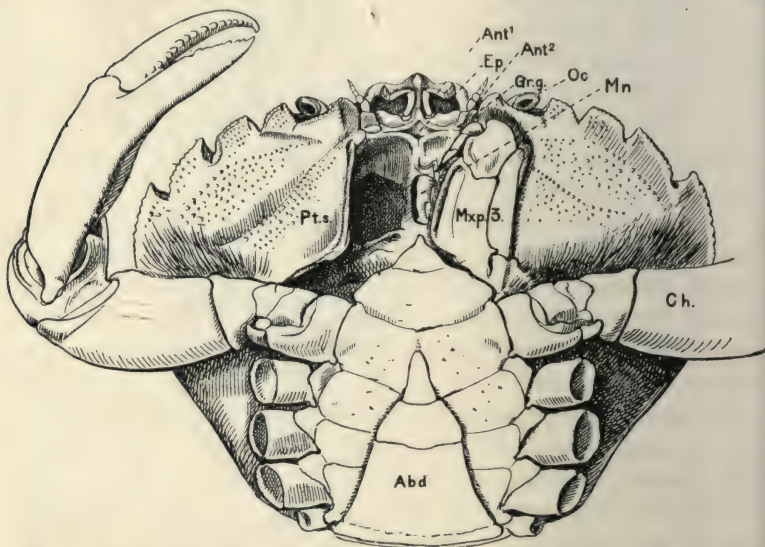


FIG. 316.—Ventral surface of *Carcinus moenas*, male, showing the relation of the pterygostomial region to the epistome in the Brachyura. The jaws and maxillipeds of the right side of the crab have been removed. *Abd.* abdomen; *ant*¹ first antenna; *ant*² second antenna; *Ch.* chelipeds; *Ep.* epistome; *Gr.g.* flap covering the opening of the green gland on the second antenna; *Mn.* mandible; *mxp. 3.* third maxilliped; *Oc.* eye; *Pt.s.* pterygostomial flap.

Another characteristic feature of the Brachyura is that the rostrum is very short and united below with the front of the epistome, by a median ridge passing between the bases of the first antennae (Fig. 316).

Orbits. In the Macrura the eye-stalks are inserted near together in front of the first antennae and the eyes project sideways. The edges of the carapace (pleura) are, as noted above, excavated to give them play.

In the Brachyura, in accordance with the transverse extension of the front of the carapace, the eyes are generally set far from

the middle line, and project externally to the second antennae (Fig. 316). They are lodged in hollows of the cephalo-thorax, the orbits, but the structures bounding the latter vary in the several groups. The anterior, external, and posterior walls of the orbit may, as we have seen, be regarded as formed by the pleural fold, the excavation of the margin having become very much deeper than it is in the *Macrura*.

In most *Brachyura* the basal segments of the second antenna are situated at the postero-internal angle of the orbit, and thus furnish a part of its boundary; the enlarged basal segments of the first antenna completing the inner walls (Fig. 316).

In the *Catometopa* the down-turned front of the carapace bounds the orbits internally, and a blunt spine-like process from the posterior orbital margin, projecting forwards and inwards, more or less completely excludes the second antenna from participation in the orbital boundary.

In the *Ocypodidae* the orbits are greatly extended laterally to form "*orbital grooves*," lodging the long and highly mobile eyes.

Finally in the *Oxystomata* there is no posterior orbital wall, the pleural fold being absent in this region.

Branchiae. In *Anaspides* each thoracic leg bears, as has been shown, two epipodial gills, having a simple leaf-like form (Fig. 287). In the larva of *Penaeus*, the branchiae make their appearance as simple lobes, of which there are at first three, attached to the bases of each of the central thoracic limbs. To these a fourth is soon added, Fig. 317, lying near the proximal one. Of the original three, the middle branchia is attached to the region which subsequently becomes the membrane of the articulation

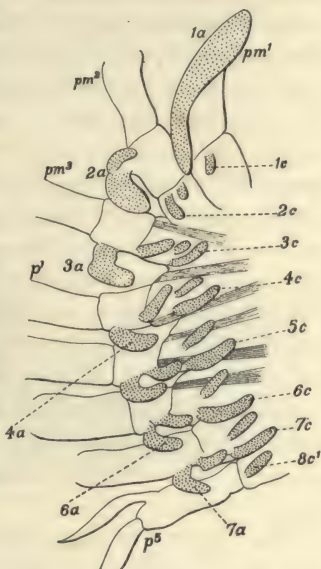


FIG. 317.—The rudiments of the branchiae of *Penaeus* (after Claus). 1a-7a podobranchiae; 1c-7c and 8c' pleurobranchiae, in most segments two to each appendage; the arthrobranchiae are seen between the podobranchiae and pleurobranchiae; p^1 - p^5 trunk legs; pm^1 - pm^3 maxillipeds.

connecting the limb with the body.* Though the base of the limb, bearing the proximal branchiae, projects in the larva, it is subsequently merged in the trunk, and hence the two branchiae which it bears are attached in the adult to the body wall (pleurobranchiae). The others, attached to the articular membrane and the basal segment of the adult limb, become the arthro- and podobranchia respectively.†

It would thus appear that the branchiae of Decapods were all originally appendages of the limbs, as are those of *Anaspides*, and that their partial change in relation is due to the fusion of the proximal segments of the limbs with the trunk—possibly owing to the formation of a branchial cavity. The distal branchial outgrowth (podobranchia) may develop into a simple plate, or into a plate bearing branchial filaments, as in *Astacus*, or into a plate bearing branchial filaments, but also extended into a process free from such filaments. Although it is probable that all the branchiae are epipodial in nature, the terms *epipodite* and *flagellum* are, in Decapod terminology, applied to the more or less tapering plate-like process of the podobranchia, which bears no branchial filaments. It is the *mastigobranch* of Spence Bates' nomenclature. Huxley uses the term *lamina* for a plate-like part of the podobranchia which bears gill filaments, as e.g. in *Astacus*.

The number of branchiae varies greatly and is not constant even in the same genus. The slender pelagic *Leucifer* is the only known Decapod without them. The number is generally largest in the Macrura Reptantia (*Palinurus* and *Astacopsis* 21, Huxley, *Astacus* 18, Huxley)‡ and smallest in the Caridea (*Pandalus* 12, *Crangon* 6, Claus) and Brachyura (*Cancer* 9, Huxley, *Pinnotheres* 3, Claus). Among the Penaeidea, *Penaeus* has 18, Claus and

* The question how the four branchiae of the limbs of Decapods are related to the two on those of *Anaspides* appears too far from solution for profitable discussion here, cf. Borradaile, l.c. pp. 461-463.

† Huxley concluded from his examination of the Crayfish that the branchial equipment of a segment was 1 podobranchiae, 2 arthrobranchiae and 1 pleurobranchiae. But Claus, from his study of the development of *Penaeus* is inclined to regard the posterior arthrobranch of Huxley as belonging to the proximal series, i.e. as a pleurobranch.

‡ It has recently been shown by Miss M. Moseley that a rudimentary posterior arthrobranch (a second pleurobranch on Claus' reckoning), at the base of the first maxilliped, is present in *Astacus fluviatilis* Fabr. (sensu stricto), which would bring the number of gills for this species to 19. See *Q.J.M.S.* Vol. 48 (1905), p. 359.

Sergestes 12, but the deep-sea form *Benthesicymus* has 24 gills.*

There are two main forms of branchiae in the Decapods, *phyllobranchiae*, consisting of simple leaflike lobes set on either side of a main axis, and *trichobranchiae* in which linear offsets are arranged around a central stem. A third type, the *dendrobranchiate*, may be regarded as a modification of the phyllobranchiate by the sub-division of the lateral lobes of the gill. It is met with, under somewhat different forms, in the Penaeidea. The Caridea and Brachyura have phyllobranchiae, the majority of the Macrura trichobranchiae, but in the Paguridea and Thalassinidea both kinds are found.

The branchiae are usually completely enclosed between the lateral fold of the carapace (*branchiostegite*) and the body wall, though their bases are often exposed in some Caridea. The water about them is renewed by the movements of the scoop-shaped exopodite of the second maxilla, known as the *scaphognathite*, which lies at the anterior end of the

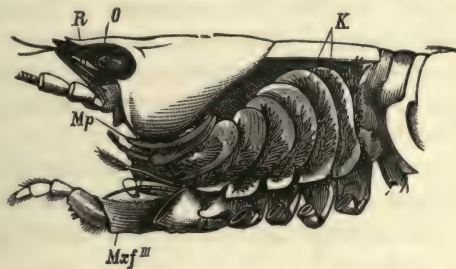


FIG. 318.—Cephalothorax of *Astacus fluviatilis*, after removal of the branchiostegite. *K* podobranchiae; *Mp* scaphognathite of second maxilla; *Mxf'''* third maxilliped; *O* stalked eye; *R* rostrum. (From Claus, after Huxley.)

branchial chamber and drives out the water which in the Macrura enters behind and below the branchiostegite (Fig. 318). In the Crabs the water usually enters the branchial chamber by an aperture situated behind the pterygostomial region, and in front of the bases of the chelipeds. The epipodite of the third maxilliped is dilated at its base into an oval plate, which regulates the flow of water into the chamber through this aperture. The sides of the carapace and the bases of the limbs in the neighbourhood of the inhalent aperture are, in sand-haunting crabs, plentifully clothed with hairs, which form, when the legs are in the

* It is customary to sum up the number of gills on one side of the body in a "branchial formula" thus: *Pandalus* 12 + 7 ep; *Penaeus* 17 (+r) + 5 ep. ep stands for epipodite or flagellum in the sense defined on p. 518, and r for a vestigial branchia.

position of rest, a filter through which the water is drawn on its way to the gills. The water driven out by the scaphognathite escapes at the antero-lateral margins of the buccal cavity.

Garstang * has called attention to the filtering mechanisms found in several groups of Decapods. In the nocturnal shore-haunting crab *Corystes*, the setose second antennae are much elongated and, when placed in apposition, form, as was recognized by Gosse and by Robertson, a straight tubular channel for the respiratory water when the body of the animal is buried in sand. Garstang finds that during the day, when it is so buried, the channel is inhalent, the water passing out at the bases of the legs, but that the direction of the respiratory stream can be reversed, during the activity of the crab, at night. A similar contrivance is found in the anomuran *Albunea*, but here the channel is formed by the first antennae. The oxystomatous crabs (p. 544) present analogous arrangements, and in many cases the shape of the carapace and the limbs is so adjusted as to provide narrow rifts through which the inhalent water is strained.

Land-crabs are provided with special arrangements for preventing evaporation in their gill chambers, but in *Birgus latro*, the branchial chambers have assumed a pulmonary character (p. 540).

Appendages. The *first antenna* consists of a three-segmented shaft (containing, except in some Caridea, the otocyst) bearing usually, as in Schizopods, two flagella of which the inner is usually the thicker and more abundantly supplied with sensory hairs. In the nauplius larva of *Penaeus* it is as usual uniramous. The Palaemonidae are remarkable in that these appendages bear, as in Stomatopods, three flagella—two of them representing the inner flagellum, and indeed uniting in a common base which bears the usual relation to the outer flagellum. In the Penaeidea and many Caridea a pointed spine-like or lamellar process, the “*stylocerite*” projects forward from the inner aspect of the basal segment of the first antenna. In the Brachyura the first antennae are usually short and contained in depressions of the frontal margin. The three segments of

* On some modifications of structure subservient to respiration in Decapod Crustacea . . . , *Q.J.M.S.*, vol. xl. (1898), p. 211. See also the literature there quoted.

the shaft are folded on themselves, and the two flagella are much abbreviated (Fig. 316 *Ant.*¹).

The *second antenna* consists typically of a two-segmented protopodite, a scale-like exopodite (*scaphocerite*), and of an endopodite ending in a flagellum. The proximal segment (coxopodite) bears the orifice of the green gland on a prominence (Fig. 314 *Doe*). The second segment (basipodite), is often divided longitudinally, when the exopodite is present, into two parts. The exopodite, though retaining its flagellar character in the larvae of some of the lower Decapods, is, when present in the adult, an undivided scale-like structure, often ending in a spine. It presents many phases of reduction and in the Scyllaridae and Brachyura is absent altogether. The endopodite has two large basal segments, the proximal articulating with both divisions of the basipodite, and a many-jointed flagellum. When the exopodite is absent the appendage presents a 4-segmented shaft ending in a flagellum.

The Scyllaridae are remarkable in that the coxopodites of the second antennae have become completely fused with the epistome, and, except for a faint median division, with one another.

In the Brachyura these appendages are much reduced, and the basipodite is often completely fixed between the epistome and the pleural margin (Fig. 316). The coxopodite appears to be still recognizable as the small opercular flap covering the orifice of the green gland. Other modifications of the second antennae and their relation to the orbits are described above (p. 516).

The *mandible* is generally robust, and the palp well developed, though the latter is absent in several families of the Caridea.

The first *maxilla* is produced inwards into two lobes, referred by Hansen (*see* p. 438) to the first and third segments of the limb.

The *second maxilla* is likewise produced inwards into two lobes, both deeply divided (Fig. 240, *d*, p. 346). The palp, though two jointed in some larvae, is unsegmented in the adult. The exopodite is expanded into a long plate, the *scaphognathite*, which, lying, as we have seen, in the channel of the outgoing water, effects, by its movements, the renewal of water in the branchial chamber.

The three anterior pairs of **thoracic legs** of Decapods have, for the most part, lost their locomotory function in the adult and are modified, as *maxillipeds*. Hence there are only five

pairs of locomotory legs on each side of the thorax. These are known as the *trunk-legs* or *pereiopods* and in reference to their number the group is named.

The biramous character is retained by the maxillipeds throughout life, and in the Penaeidae and some Caridea a reduced exopodite persists on the trunk-legs, but in other Decapods exopodites are wanting from the trunk legs in the adult, though appearing in the 'Mysis' stage of many Macrura.

The endopodites of the third maxillipeds retain something of a leg-like character in the Macrura (Fig. 314, *max*³), although they are no longer used in locomotion, but in the Brachyura these appendages become broad and opercular, folding together over the mouth parts anterior to them, like doors (Fig. 316).

The exopodites of the maxillipeds of the Brachyura end in whip-like appendages directed backwards over the gills, and the bases of those of the first and third are expanded into plates which control the current of the respiratory water. The characters of the endopodites of the first maxillipeds of the Oxystomatous Brachyura are mentioned on p. 544.

The first maxilliped of the Caridea is peculiar in the possession of an unsegmented lobe on the outer border of the exopodite. The first trunk-legs (*chelipeds*) are generally chelate, but this character is often shared by their successors.

In connexion with the problem of segmentation attention may be drawn to the remarkable multiarticulate character of the carpus (antepenultimate segment) of the second trunk-leg in the Hippolytidae, and other families of the Caridea.

Of the *abdominal appendages* the last pair (*uropods*) form with the telson the powerful swimming tail fin of the Macrura. The pleopods are best developed in the Macrura Natantia, where they are the locomotory organs in ordinary swimming. In the Caridea a small lobe known as the *appendix interna* and projecting on the inner margin of the endopodite is constantly present (the "*stylambis*" of Spence Bate's terminology). We have already met with this appendage in the Leptostraca and Euphausiidae (pp. 458 and 467). Among Decapods it is absent in the Penaeidea, Nephropsidae, and Brachyura, but appears in the Caridea, Eryontidae and Scyllaridae, most Thalassinidea (Fig. 319) and some other Anomura.

The first and second abdominal limbs of the male are modified

as copulatory organs in the Nephropsidae, Galatheidea and the Brachyura, but in the Caridea and Scyllaridae this is never the case. The other abdominal limbs are more or less reduced or absent in the higher Decapoda, though some are generally retained in the female for the support of the eggs and young.

The **nervous system** of Decapods is referred to at p. 443, and the sense organs at pp. 328ff and 350. A glimpse into the high psychological development attained by the Brachyura is afforded by the remarkable habit possessed by many of the Oxyrhyncha of decking themselves (cf. p. 544) with pieces of seaweeds and colonial animals (such as *Alcyonium* and Ascidians) among which they live. They thus by their own activity attain a result, that of blending in appearance with their environment, which in *Hippolyte varians* is attained by a complex reflex action (p. 444).

The **heart** is perforated by three pairs of ostia, two dorsal and one ventral. An anterior median artery carries the blood to the brain and eyes, and anterior paired arteries supply the antennae. Paired *hepatic* arteries ventral in origin supply the stomach,



FIG. 319.—Third abdominal limb of *Azius acanthus*. 1 endopodite; 2 appendix interna ("stylambis"). After Borradaile.

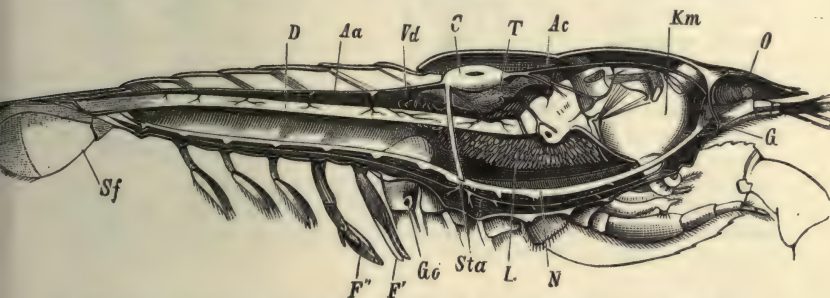


FIG. 320.—Longitudinal section through *Astacus fluviatilis* (from Claus, after Huxley). Aa abdominal aorta, the sternal artery (*Sta*) is given off close to its origin; Ac cephalic aorta; C heart; D intestine; G brain; Gg genital opening; Km masticatory stomach; L liver; N, ganglionic cord; Sf lateral plate of the caudal fin; T testis; Vd vas deferens.

liver and gonads, and a median abdominal artery carries the blood to the hind end of the body. The unpaired *sternal* artery descends vertically, passes through the ganglionic chain and divides into anterior and posterior trunks which run above the sterna of the

segments (Fig. 320, *Sta*). From the arterial capillaries the blood collects into sinuses at the bases of the gills, and after its oxidation, returns by branchial veins to the pericardial sinus.

Alimentary Canal. The masticatory stomach is large and complex in Decapods. The many-lobed *digestive gland* of the adult is derived from three pairs of simple diverticula in the larva, and, with the pyloric stomach into which it opens, represents the larval hypoblast.

Excretory Organs. The antennal glands consist of a glandular sac (*sacculus*) which communicates with the external opening at the base of the second antenna by a contorted *glandular duct*, usually dilated before its termination into a *receptaculum*. The sacculus has been interpreted as homologous with the end-sac of the nephridium of *Peripatus* (see p. 542). The parts present great variation in different groups.

In *Astacus* the apparatus is disposed in two oval masses lying one above the other; dorsally is placed the receptacle, opening in front on the 2nd antenna, and ventrally the glandular mass, of complex structure, and containing the sacculus (yellow) embedded in its upper portion. The duct after leaving the sacculus expands into a complex network of tubes (labyrinth), with green granules in the cells, which forms a cortical layer over the lower surface of the organ. The labyrinth opens

into a tangled tube occupying the inner (white) portion of the organ, and opening posteriorly into the receptaculum.

The receptaculum is rarely as simple as in *Astacus*, but sends out diverticula, which may unite, as in *Pagurus Bernhardus* into a median tube, extending back as far as the last quarter of the abdomen.

Reproductive organs. The arrangement of the gonads and their ducts is shown in Fig. 321. The spermatozoa of Decapods

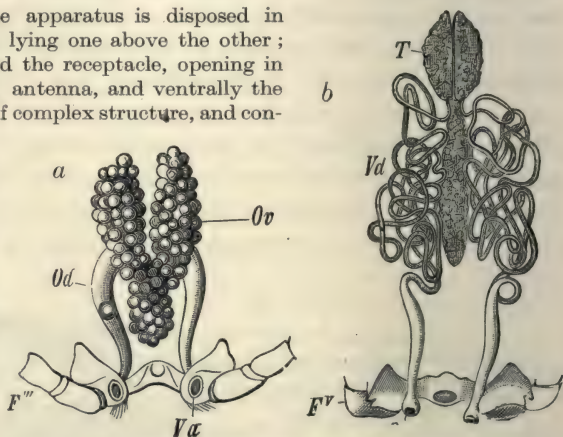


FIG. 321.—Generative organs of *Astacus* (after Claus). *a* female; *b* male. *Od* oviduct; *Oe* genital openings of the basal joint of the fifth pair of ambulatory legs (*Fv*); *Ov* ovaries; *T* testis; *Va* vulva on the basal joint of the third pair of ambulatory legs (*F'''*); *Vd* vas deferens.

are contained in *spermatophores*, the material of which is secreted by the vasa deferentia (Grobben). The sperm from one side may be carried in a single spermatophore, as in many *Brachyura*, etc. In the crayfish (*Astacus*) the secretion hardens on coming in contact with water into the chalky white substance which may often be found on the under surface of the female.

The **spermatozoa** have long been recognized as exceptional in that they are without a vibratile flagellum, they are usually beset with three or more diverging processes, and they are deprived of the power of independent locomotion. Light has been thrown on the function of these remarkable structures and the relation of their parts to those of other spermatozoa, by Koltzoff (l. c.) who has examined their development in particular cases.

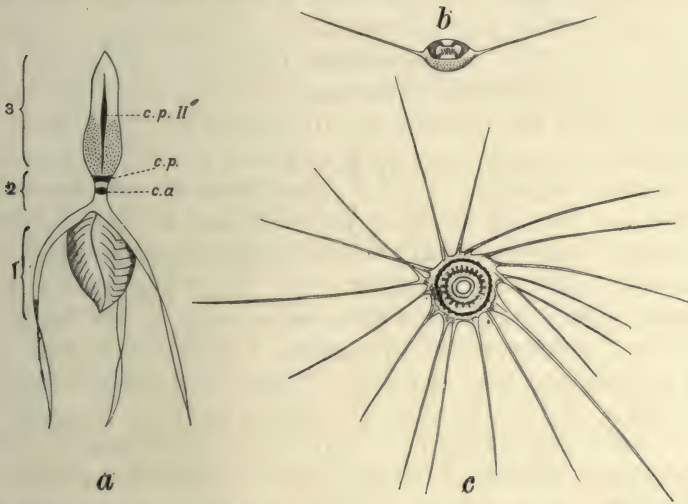


FIG. 322.—Decapod spermatozoa. *a*, spermatozoon of *Galathea squamifera* (after Koltzoff). 1 head; 2 neck, with processes; 3 capsule; *c.a* anterior centrosome; *c.p* and *c.p II* anterior and posterior division of posterior centrosome. *b*, spermatozoon of *Astacus fluviatilis*, showing the capsule sunk in the head. *c*, the same, seen from above, and more highly magnified (after Grobben).

Fig. 322 *a* represents a spermatozoon of the Anomuran *Galathea squamifera*. It consists of (1) a large head (represented below in the figure), containing the nucleus; (2) a neck, the constricted part at the base of the head, containing the anterior centrosome and produced into three long processes, which, though so rigid that they can support the spermatozoon as on a tripod, are capable of contraction, and at their tips at any rate are highly adhesive;

and (3) the capsule, corresponding to the region of the tail. The last contains the two parts of the posterior centrosome which lie in the "pars conjunctionis" or basal region of the tail of an ordinary spermatozoon. The capsule consists of an outer "chitinous" envelope, an inner "chitinous" tube investing the second division of the posterior centrosome, and of a substance between (partly dotted in Fig. 322 *a*), capable of swelling quickly in water. The swelling leads to sudden inversion of the parts of the capsule, a result which is accomplished with "explosive" rapidity.

Koltzoff finds that the spermatozoa, borne in a current of water, on coming in contact with an egg adhere by the tip of one process, then by a second, and finally by all three. By a shortening of the processes the head is brought down to touch the egg membrane, and then, propelled by the "explosion" of the capsule, the head and the part of the neck containing the anterior centrosome are made to penetrate the membrane. This is regarded as the normal mode of fertilization. It should be stated however that the subsequent nuclear changes have not been followed.

Koltzoff divides the spermatozoa of Decapods into *anacantha* which are without diverging processes and are found in the Natantia, and *acanthina*, found in the other groups, and provided with such processes. The latter are divided into *cephalacantha* in which the processes spring from the region of the head (Brachyura) and *deracantha* * in which they spring, as in *Galathea*, from the neck. Finally the latter are again divided into *erecta*, in which the several parts are arranged, as in *Galathea* (Fig. 322 *a*), in a linear series, and *contracta* in which the capsule, with an intervening layer representing the neck is sunk into a depression of the head—the whole having, as in the case of the crayfish, the shape of a sphere with diverging processes (Fig. 322 *b* and *c*).†

The sexes are distinct in the Decapoda, though sexual dimorphism is less marked than in many groups of Crustacea. The males are more abundantly supplied with olfactory hairs than

* *δερν* the neck.

† As spermatozoa *acanthina*, *deracantha*, *erecta* Koltzoff classifies those of the Paguridae, Galatheidea and *Homarus* (the lobster), while the Loricata, Thalassinidea and the crayfish (*Astacus*, Fig. 322 *b*) have according to him spermatozoa *acanthina*, *deracantha*, *contracta*—a difference between the lobster and the crayfish which may raise a doubt as to the far-reaching character of the distinction.

the females and are also distinguished by the narrower shape of the abdomen (Fig. 314), as well as by the position of the openings of the vasa deferentia on the last thoracic segment, and, in the higher Decapods, by the modification of the first and second pleopods as copulatory organs. In the males of the *Brachyura* the pleopods behind the second pair are absent in the adult. The remarkable effect on the gonads and secondary sexual characters of Decapods caused by parasitism are described on p. 415.

In the *Penaeidea* the eggs are hatched at a very early stage, and the females of this group have not been found carrying their eggs. In all other Decapods the brood is carried by the female on certain pairs of pleopods, either beneath the outstretched abdomen, or between the bent abdomen and the thorax. The pleopods are longer than in the males, and fringed, especially the basal segments and the endopodites, with long hairs. The eggs are attached by a sticky secretion to the surfaces or hairs of the pleopods or to one another. The young of the fresh-water crayfish have hooked ends to the blades of the chelae, by which they cling without effort to the empty egg membranes or hairs of the mother.

The *Penaeidae* present peculiar structures which are apparently sexual in character. In *Penaeus*, *Leucifer* and *Sergestes* a lobe projects inwards from the base of the first pleopods of the male, and may unite with its fellow to form the *petasma* (or curtain) (Spence Bate). In the female *Penaeus* two lobed structures have been found in connection with the 7th and 8th thoracic sterna, in the middle line and projecting forwards. They constitute the *thelycum* of Spence Bate. Both this and the *petasma* are apparently variable in configuration and we have no direct information as to their functions.* The larval stages of Decapods are alluded to above (p. 448) and some of them are figured in the sequel.

Section 1. MACRURA NATANTIA.

Body more or less compressed, abdomen well developed. First abdominal segment not markedly smaller than the next.

* The author is informed by Mr. W. T. Calman, to whom he is indebted for many valuable criticisms, that the *thelycum* is almost certainly an external spermatheca, like that found in *Cambarus* and *Homarus*.

A long compressed rostrum is usually present. First antenna usually bears a stylocerite. Second antenna usually with a

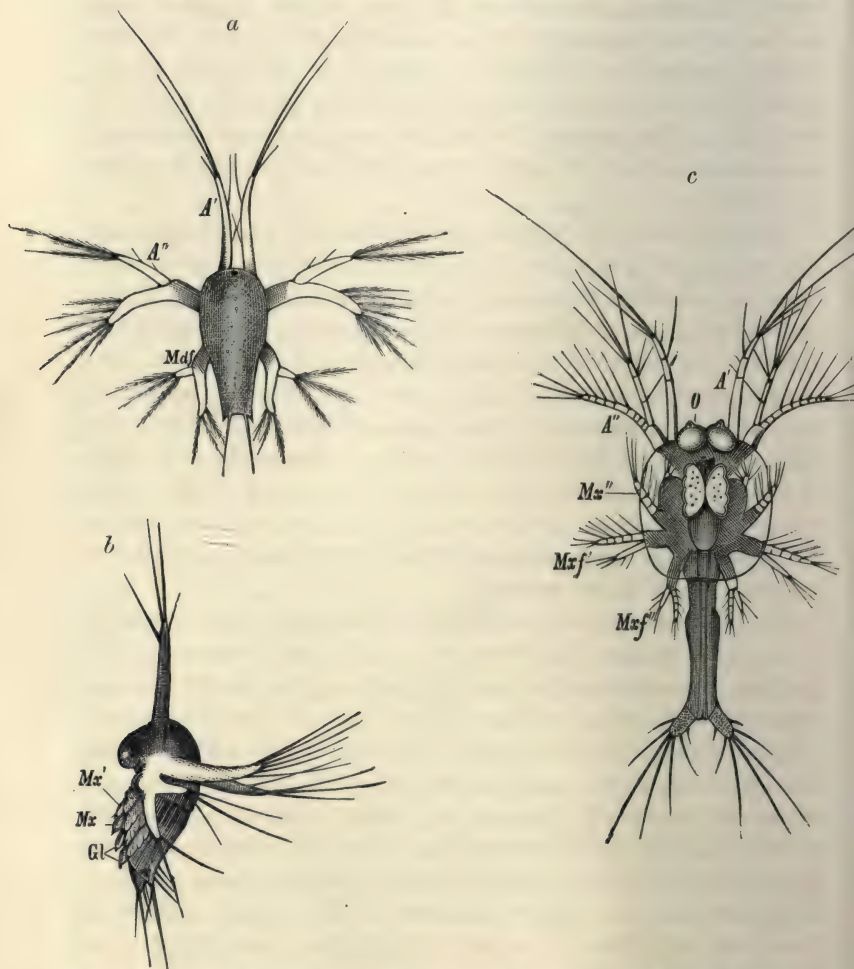


FIG. 323.—Larvae of *Penaeus*. (From Claus, after Fritz Müller.) *a*, nauplius form seen from the dorsal surface. *b*, metanauplius stage seen from the left side; *c*, zoaea stage; *A'*, *A''* first and second antennae; *Gl* sixth and seventh pairs of appendages (first and second maxillipeds); *Mdf* mandibular palp of nauplius; *Mx'* anterior maxillae; *Mx''* posterior maxillae; *Mxf'*, *Mxf''* first and second maxillipeds; *O* eyes.

large flat scale (exopodite). Thoracic legs slender, abdominal legs powerful swimming appendages.

Tribe 1. **PENAEIDEA.**

Gills dendrobranchiate. The 1st abdominal segment not overlapped by the 2nd, 1st antenna usually with a stylocerite. The 3rd and frequently

the two preceding trunk-legs chelate. Abdomen long. The larvae hatch either in the nauplius (*Penaeus*), metanauplius (*Leucifer*) or protozoaea (*Sergestes*) stage.

Fam. 1. **Penaeidae**. In most the three anterior trunk-legs retain flagelliform exopodites (as in Schizopods), and an epipodial plate, which is however usually without branchial filaments. They are chelate, and successively increasing in length; their antepenultimate segments long. The branches of the gills bear multifid or arborescent subdivisions. Rostrum present; posterior part of abdomen dorsally carinate; first abdominal segment overlaps the second at the sides. Eye stalks 2 or 3-jointed; mandibular palp broad, 2-jointed. Several Jurassic genera (Boas). *Penaeus* Fab., flagella of 1st antennae shorter than carapace; *P. caramote* (Risso) Mediterranean, occasionally British. *P. esculentus* Hasw., the edible prawn in Sydney, N.S.W. *Penaeopsis* Sp. B. *Solenocera* Lucas, 1st antennae modified to conduct the efferent respiratory water. *Parasolenocera* W.-M. and A.; *Hymenopenaeus* Smith; *Haliporus*, *Artemesia* and *Philonicus* Sp. B.; *Parapenaeus* Smith; *Metapenaeus* W.-M. and A. *Sicyonia* M. Edw., exopodites of trunk-legs absent; littoral. The 6 genera *Aristeus* Duv., with branchiate epipodites to the 2nd-6th thoracic legs, *Aristaeopsis* and *Aristaeomorpha* W.-M. and A., *Hemipenaeus* and *Hepomadus* Sp. B., and *Benthescymus* Sp. B., inhabit the deep sea. *Gennadas* Sp. B., also from the deep sea with supplementary lens to the eye. A genus described as *Peteinura* by Spence Bate has exopodite of 6th abd.-appendage immensely elongated in larva.

Here may be mentioned a remarkable form—*Cryptopus* Lat. (= *Cerataspis* Gray) a pelagic Crustacean, 8 mm. long, which has been obtained from the stomachs of fishes (bonito and "dolphin" (*Coryphaena*)). The carapace is inflated and its sides nearly meet ventrally. Seven biramous thoracic legs are present, bearing at their bases simple or compound phyllobranchiate gills. The nauplius stage is apparently passed before the young escape from the eggs, which are attached to the thoracic legs and sheltered in the carapace.

Fam. 2. **Sergestidae**. With elongated bodies and slender limbs. Mandibular palp 2-jointed. 2nd and 3rd maxillipeds pediform. The trunk-legs have lost their exopodites, the epipodites are also absent and the 4th and 5th are reduced or absent. Gills when present, reduced in number, with simple lamellar subdivisions of the branches of the main axis. Chelae of the trunk-legs minute. First abdominal appendages of male modified as copulatory organ. *Sergestes* M. Edw. Two posterior pairs of trunk-legs reduced. Flagellum of 2nd antennae very long. Arthrobranchiae absent. Stages in the remarkable metamorphosis known as *Elaphocaris* (protozoaea and zoaea), *Acanthosoma* (mysis stage) and *Mastigopus*. Many spp. pelagic, and widely distributed, but one found by Graham Kerr, on the Rio Parana, S. Am., several hundred miles from the sea. *Acetes* M. Edw. *A. indicus* M. Edw. Last trunk-legs 0, 4th reduced. Mouth of the Ganges. *Petalidium* Sp. B., arthrobranchiae on 5 pairs of anterior thoracic legs. *Leucifer* M. Edw. Cephalic region and eye-stalks much elongated, and thoracic region very short. 4th and 5th trunk-legs 0. Gills 0. Phosphorescent. Young hatched in metanauplius stage. The metamorphosis through protozoaea (*Erichthina*), zoaea, mysis, and mastigopus stages has been followed by Brooks (Fig 324).

Amphion. The singular pelagic forms referred to this genus have a transparent flattened carapace, and elongated thoracic appendages, recalling the Phyllosoma larvae of the Loricata (cf. p. 535), though they differ from

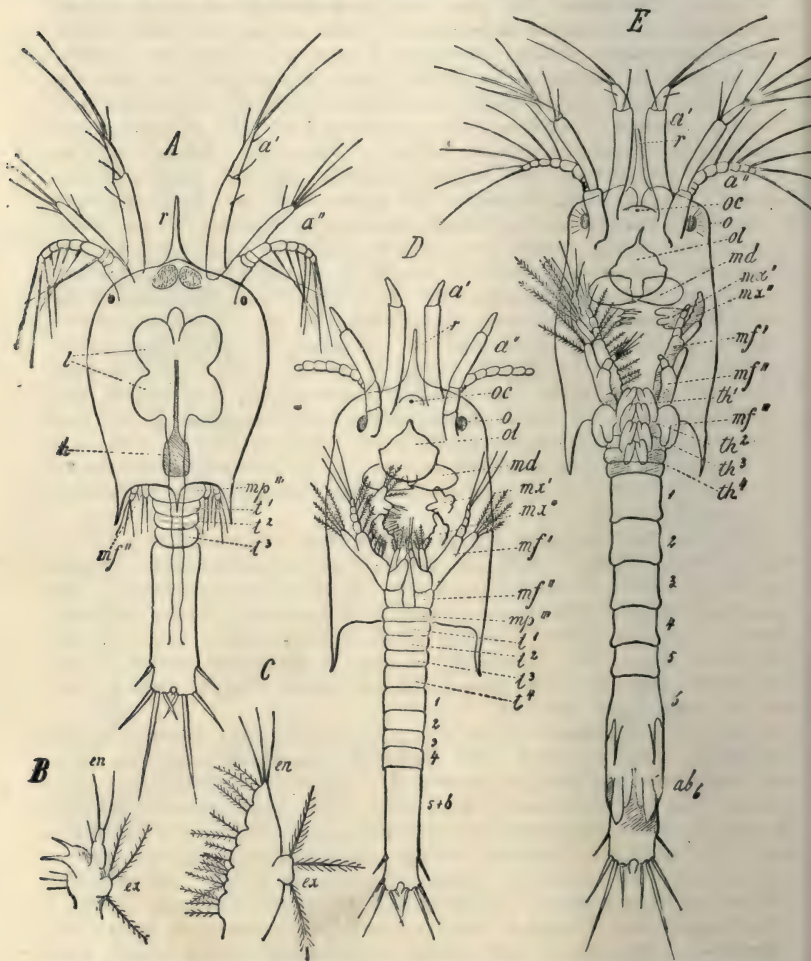


FIG. 324.—Protozoaeae and Zoea larva of *Leucifer*. A, first protozoaea stage; B, first maxilla of the same; C, second maxilla of the same; D, later protozoaea stage (*Erichthina*); E zoea stage; *a'* first antenna; *a''* second antenna; *ab₆* uropods; *en* endopodite; *ex* exopodite; *h* heart; *l* hepatic outgrowths; *md* mandible; *mf'*, *mf''*, *mf'''* first, second and third maxillipeds; *mp'''* third thoracic segment; *mx'* first maxilla; *mx''* second maxilla; *O* paired eye; *oc* nauplius eye; *ol* upper lip; *r* rostrum; *th¹*–*th⁴* rudiments of the first to the fourth trunk-legs; *tl¹*–*tl⁴* the segments carrying them; 1–6 the six abdominal segments. (From Korschelt and Heider, after Brooks.)

them in the absence of a constriction in the cephalo-thorax. The first thoracic limbs are maxillipeds and grouped with the oral appendages, apart from the other thoracic legs. The latter are elongated biramous structures; but the last (8th) is small and rudimentary in *A. Reynaudii*,

absent in *A. provocatoris*. The uropods form with the telson a powerful tail fin, but the other abdominal appendages are rudimentary or absent. The gills are phyllobranchiate. A zoea form of *Amphion* is known, but it is not certain, notwithstanding the presence of ovaries, and indications of testes in the most fully developed examples known, whether they have attained the adult structure.

Tribe 2. STENOPIDEA.

Gills numerous and trichobranchiate. First abdominal segment not overlapped by second. 1st antenna without stylocerite. Mandible undivided, with a palp. First maxilliped without the characteristic lobe of the Caridea. Swimmerets not coupled.

Fam. 1. **Stenopidae**. Body robust, flagella of antennae long. Ant. 2 has a large scale. Mandibular palp 3-jointed. 3rd maxilliped pediform, 7-segmented, with a slender exopodite. Trunk-legs uniramous but with epipodial plates, the 3 anterior pairs chelate, increasing in length and thickness from before backwards. Branchiae trichobranchiate.

The larva of *Stenopus* is hatched in the protozoea stage and in the course of the metamorphosis the 4th and 5th trunk-legs are reduced (compare Sergestidae) and then grow again. *Stenopus* Lat., *S. hispidus* Ind. Ocean; *Spongicola* de Haan, *S. venusta* inhabits *Euplectella* and other sponges. *Aphareus* Paulson.

Tribe 3. CARIDEA (Eucyphidea Ortm.).

1st antenna with stylocerite. First maxilliped with a characteristic lobe on the outer border of the exopodite and terminal segments of its endopodite generally expanded or distorted. Gills phyllobranchiate. The first and second trunk-legs often, the others never chelate. The second abdominal segment overlaps its neighbours laterally; the endopodites of the swimmerets coupled to their fellows by appendices internae. The larva is usually hatched as a zoea in which all three pairs of maxillipeds are present as biramous swimming appendages (Fig. 325). A mysis stage frequently follows.

Fam. 1. **Pasiphaeidae**. Laterally compressed, with large abdomen; rostrum small or 0. Trunk-legs with exopodites, three posterior pairs reduced. Moderate depths to deep water. *Psathyrocaris* W.-M.; *Pasiphaea* Sav. 2nd and 3rd maxillipeds pediform. *P. sivado* (Riss.) British. *P. princeps* S. I. Smith. 9 in. Atlantic. *Leptochela* Stimps. The genera *Parapasiphae* S. I. Smith. *Orphanisa* Sp. B.; and *Phye* W.-M. and A. are deep-sea forms.

Fam. 2. **Bresiliidae**. Rostrum well developed; only the 1st and 2nd trunk-legs with exopodites. Terminal segments of 2nd maxilliped not expanded or distorted. *Bresilia* Calman. Deep water, West of Ireland.

Fam. 3. **Acanthephyridae**. Laterally compressed and dorsally carinate; rostrum prominent, laterally compressed; mandibular palp 2-3 jointed; trunk-legs with exopodites and reduced epipodites. *Bentheocaris* Sp. B.; *Acanthephyra* A. M. Edw. from the surface to 3,000 faths., some phosphorescent; *Systellaspis* Sp. B.; *Hoplophorus* M. Edw. scale of 2nd antenna large, capable of being fixed, as an offensive weapon; *Notostomus* A. M. Edw.; *Ephyrina* Sm. (= *Tropiocaris* Sp. B.); *Hymenodora* Sars; *Nematocarcinus* A. M. Edw. with the 4 posterior trunk-legs immensely elongated, deep water.

Fam. 4. **Atyidae**. Mandibles without palps; 3rd maxillipeds pediform,

4-jointed; 1st and 2nd trunk-legs with highly mobile chelae having spoon-shaped tips beset with brushes of long setae, the carpal segments short and crescentic; reduced epipodites on 4 anterior trunk-legs, exopodites on trunk-legs in the first three genera. Many closely related species distributed in fresh-water lakes in different parts of the world, some in oceanic islands. *Troglocaris* Dormitzer, in caves in Corinthia; *Xiphocaris* v. Marts. W. Indies to Queensland; *Atyaephyra* Brito-Capello, S. Eur.; *Caridina* M.-E. some 20 spp. Indo-Malay, Africa, and W. Ind. *Atyoida* Randall; *Atya* Leach, some 6 spp. scattered round the world in tropics; *Limnocaridina* Calm. Lake Tanganyika, gills only 4 on a side.

Fam. 5. **Stylodactylidae** Sp. B. Deep sea forms, with the 2nd maxillipeds terminating in 2-lobed divisions, and the two anterior pairs of trunk-legs with long and tapering divisions of the chelae. *Stylodactylus* A. M.-E. 4 spp. ranging down to 600 faths. Pac. and W. Ind.

The five following families, grouped about the central Hippolytidae usually have the carpus of the 2nd trunk-legs multiarticulate (as also have the Processidae, see below), except Rhynchocinetidae and some others.

Fam. 6. **Alpheidae**. Rostrum small, eye stalks covered by the edge of the carapace. Mandible with a 1-2-jointed palp. First trunk-legs with robust unsymmetrical chelae, with which some species make a peculiar snapping noise; second with minute chelae; the 4 anterior pairs bear rounded epipodites. *Alpheus* Fab. widely distributed, *A. comatularum* Hasw. associated with a Comatulid which it resembles in colour. *A. ruber* M. Edw. British and Mediterranean. *Athanas* Leach, *A. nitescens* Leach, British. *Alope* White.

Fam. 7. **Psalidopodidae**. 1st trunk-legs, with both blades of the chelae movable, 2nd not chelate. Body beset with strong spines. *Psalidopus* W.-M. and A. 2 spp. Indian Ocean, 400-500 fthms., with rudimentary eyes.

Fam. 8. **Pandalidae**. Rostrum long; palp of mandible 2-3-jointed; 1st trunk-legs not chelate and only 6-jointed; the chelate 2nd pair sometimes unequal. *Pandalus* Leach, 4 British spp.; littoral and deep sea. (Doubtful genera *Heterocarpus* and *Chlorotocus* A. M.-E.; *Nothocaris*, *Pandalopsis* and *Dorodotes* Sp. B.) *Thalassocaris* Stimps. carpus of 2nd trunk-legs unjointed, powerful chelae. 2 spp. Trop. Pac. (*Diaphoropus*, *Kyptocaris* and others of Spence Bate's genera are larval forms.)

Fam. 9. **Hippolytidae**. Rostrum large, eyes prominent, mandibular palp present or 0; 1st trunk-legs chelate, short and robust, the 2nd chelate but more slender, its carpus subdivided into 2-very many joints,

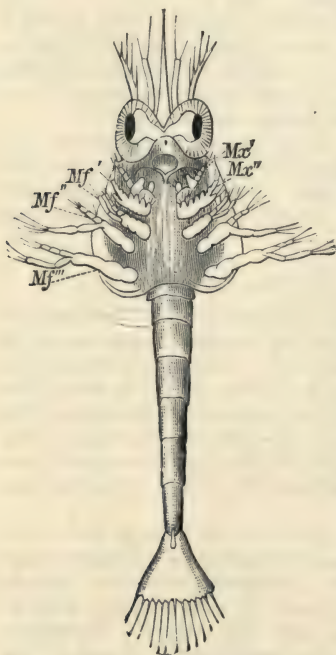


FIG. 325.—Zoaea of *Hippolyte*. *Mf* *Mf'*, *Mf''* first, second and third maxillipeds; *Mx'* first, *Mx''* second maxilla. (After Claus.)

according to the number of which the family is subdivided as follows : (a) 2 joints. *Caridion* Goës, Eur. (b) few jointed. *Virbius* and *Ogyris* Stimpson, with long slender eye stalks, 3 spp. E. Asia and W. Indies. *Pterocaris* Heller. 1 sp. Amboyna. Cephalo-thorax and the 3 ant. fused abdominal segments expanded into lateral wings. (c) 7—many jointed. *Hippolyte* Leach, many spp. widely distributed over the world. *H. varians* Leach, British, common in tidal pools, has the power of changing its colour according to its surroundings (p. 444). *Spirontocaris*, *Merhippolyte*, *Chorismus*, *Hetairus* of Sp. B., *Saron* Thallwitz, and *Hetairocaris* de Man. *Nauticaris* Sp. B.; *Platybema* Sp. B.; *Concordia* Kingsley; *Latreutes* Stimps.; *Tozeuma* Stimps.; *Lysmata* Riss. *Cryptocheles* and *Bythocaris*, from great depths, the young being hatched with the full number of appendages, were described by G. O. Sars, but are regarded as doubtful genera by Ortmann.

Fam. 10. **Rhynchocinetidae**. Closely allied to *Hippolyte* but the rostrum is articulated with the carapace, and the 2nd trunk-leg has the carpus not articulated. *Rhynchocinetes* M. Edw.

The two following families form an off-shoot from the Hippolytidae, characterized by having the blade of the mandible divided, the two anterior pairs of trunk-legs chelate, the second larger than the first, and the carpus not articulated, no epipodites on the trunk-legs, and the first antennae often 3-ramous.

Fam. 11. **Pontoniidae**. Rostrum broad at base; 1st antenna split at the tip; palp of mandible usually 0, 3rd maxilliped pediform, broad at the base (opercular); 2nd trunk-legs unequal, one very large in male. Littoral forms, often half parasitic. (a) mandible without palp. *Pontonia* Latreille. *P. custos* Forsk. lives between the valves of the shell of *Pinna*; *P. meleagrinae* (Pet.) in the Pearl Oyster. *Typton* Costa. *T. spongicola* Costa, lives in sponges; British. *Anchistia* Dana, *A. lacustris* v. Mart. fresh-water, Italy. *Coralliocaris* Stimpson, Ind. Pac. (b) Rostrum compressed; 1st antenna expanded into a flattened lobe; 3rd maxilliped with leaf-like flattened joints, mandible with palp. *Hymenocera* Latreille, Ind. Pac.

Fam. 12. **Palaemonidae**. Rostrum large, compressed, serrated; 1st antennae with 3 flagella; palp of mandible usually present; 3rd maxilliped leg-like. *Leander* Desm. (*Palaemon* Fabr. pars). *L. serratus* (Fabr.) the prawn of the markets. *Palaemon* Fabr. pars, 2nd trunk-legs much elongated, especially in the male, tropical fresh-waters. *P. heterochirus* Wiegman, of Mexico, 2 feet long including the legs. *P. potiuna* hatches with the appendages of the adult, except the uropods (Fr. Müller). *Palaemonella* Dana. *Palaemonetes* Heller. *P. varians* (Leach). Fresh and salt water. It has been found that while N. European forms of this species, living in the sea and brackish water, hatch in the usual zoea form (Boas), S. European specimens inhabiting streams have, at hatching, all the appendages except the uropods, and only the two anterior pairs of trunk-legs bear exopodites (P. Mayer), the metamorphosis of the fresh-water form being abbreviated.

The 3 following families form an offset from the Hippolytidae in another direction, characterized by having the blade of the mandible simple, and its palp absent, the inner lobes of the 2nd maxilla much reduced, and no epipodites on the trunk-legs.

Fam. 13. **Processidae** (= **Nikidae**). Rostrum flattened above; 3rd maxillipeds slender; 1st trunk-legs either chelate on one side only (*Processa*),

or subchelate on both sides (*Glyphocrangon*); 2nd pair minutely chelate with a many-jointed carpus. *Processa* Leach (= *Nika* Risso) a few littoral old world spp. *Glyphocrangon* A. M.-Edw. *G. rimapes* Sp. B. with large eyes, 1,715 faths.

Fam. 14. **Crangonidae**. Rostrum short and flat, 3rd maxillipeds slender; 1st trunk-legs strong and subchelate, the 2nd and 3rd slender and reduced. *Crangon* Fab. *C. vulgaris* L., the common shrimp. Sandy shores of N. Hemisphere, resembling in colour the sand in which they bury themselves. *Nectocrangon* Brandt; *Pontophilus* Leach; *Pontocaris* Sp. B.; *Sabinea* Owen, Arctic Ocean. *Prionocrangon* W.-M. and A.; *Paracrangon* Dana, 2nd trunk-legs obsolete. In *Sclerocrangon* Sars (*S. boreas*) Sars found that the young are hatched in the adult form.

Fam. 15. **Gnathophyllidae**. Rostrum compressed; 3rd maxillipeds very broad and foliaceous; first trunk-legs chelate, smaller than 2nd. *Gnathophyllum* Latreille, 5 spp. *G. elegans* Mediterranean.

Section 2. MACRURA REPTANTIA.

Body not laterally compressed; abdomen well developed, the first segment smaller than that which follows it, its pleura clipping the carapace. Tail fin broad. Scale of second antenna rarely flat, often spine-like, or absent. The first and third pairs of trunk-legs, chelate or simple. The legs of the last thoracic segment do not differ greatly from the others, and its sternum is rarely free.

The first and second families agree in the following characters. Pterygostomial regions of the carapace fused in front with the epistome. Rostrum small or wanting (except *Palinurellus*). Inner lobes of 2nd maxilla and 1st maxilliped reduced. An appendix interna on some of the abdominal legs, at least in the female, but the exopodite of the last pair is without a distinct suture.

Fam. 1. **Eryonidae**. Carapace clipped by the 1st abdominal segment alone. First joint of 2nd antenna not fused with the epistome, and a scale-like exopodite is present. Unbranched limbs on 1st abdominal segment. Tail fin without sutures. Telson pointed. Carapace depressed with a lateral ridge of spines ending in front in a large forward-pointing spine on the outer side of the empty orbit. Trunk-legs all chelate (except in male of *Polycheles*), the first longest. Deep-sea forms, blind or nearly so, found living on Globigerina ooze; allied to *Eryon* a fossil of the Lias and the Lithographic Stone of Bavaria (Upper Oolite). *Polycheles* Heller (= *Pentacheles* and *Stereomastis* Sp. Bate); *Willemoesia* Grote.

Fam. 2. **Scyllaridae** (= **Loricata**). Carapace gripped between a lobe on the 1st abdominal segment and a knob on the side of the last thoracic segment; first joint of 2nd antenna fused with epistome, and the appendage bears no scale. None of the trunk-legs much longer than the rest, and none chelate except the first pair in some cases, and the last in the females. No legs on 1st abdominal segment. Tail fin with indistinct sutures. Robust heavily-armoured forms ranging from shallow water to a depth of several fathoms. The larva undergoes a remarkable metamorphosis, being hatched as a flattened leaf-like creature, as clear as glass, known as

Phyllosoma. The 3 foremost pairs of trunk-legs are developed, and biramous (Fig. 326). It corresponds with the early mysis stage of other forms.

Sub-fam. 1.

Scyllarinae. On sandy bottoms. Body depressed; 2nd antenna a broad plate without flagellum. Orbits complete. *Scyllarus* Fab. rostrum prominent and cephalo-thorax longer than broad.

S. latus Lat.; *Thenus* Leach, rostrum bilobed, cephalo-thorax broader than long, orbits at antero-lateral angles. *T. orientalis* Fab. *Ibacus* Leach, cephalo-thorax much broader than long, orbits near the middle line. Widely distributed in warm littoral waters. *Arctus* Dana, rostrum very short, and 2nd antennae remote from one another. *A. ursus* Dana, British Isles to Australia and Japan.

Sub-fam. 2. **Palinurinae.** On rocky bottoms. Body subcylindrical, and antennae with a long flagellum. Orbits incomplete. *Palinurus* Fab. with a small rostral spine, and short flagella to 1st antennae. *P. vulgaris*, Lat., the Rock Lobster, French *languste*, coasts of Europe. Stridulating organ, on base of 2nd antennae, produces a squeaking sound. *Jasus* T. J. Parker (*Palinositus* Sp. B.) rostrum short. S. Hemisphere. *Linuparis* White, from Japan. *Panulirus* White, rostrum very small, flagella of 1st antennae long, the region bearing these appendages produced in front of the frontal margin; stridulating organ as in *Palinurus*. *Palinurellus* von Martens, rostrum covering the bases of the eye-stalks and antennae.

Fam. 3. **Nephropsidae.** Carapace free from the epistome. Rostrum of good size. Inner lobes of 2nd maxillae and 1st maxillipeds not reduced. No appendix interna. The exopodite of the last abdominal limb divided by a suture. Body subcylindrical. Carapace gripped by the 1st abdominal segment only. 1st joint of second antenna free. A scale-like exopodite is present. Three foremost trunk-legs chelate; the first pair longest. Telson firm, squared, often sutured.

Sub-fam. 1. **Nephropsinae.** Carapace subcylindrical, with rostrum; sternum of last thoracic segment ankylosed with seventh; 2nd-6th thoracic legs carry simple epipodial plates with branchial filaments springing only from their bases. Exopodite of uropod with a transverse suture. *Nephrops* Leach. *N. norvegicus* (L.), Norway lobster, also British. Branchia of epipodite of 2nd maxilliped small or absent. *Eunephrops* S. I. Smith; *Homarus vulgaris* M. Edw.



FIG. 326.—*Phyllosoma* larva of *Palinurus*. *a* d abdomen; *L* liver; *II* second, *III* third maxilliped; *IV*–*VI* the first three ambulatory legs. (From Korschelt and Heider, after Claus).

(= *Astacus gammarus* L.), the lobster. *H. americanus* M. Edw., with 2 spines on under side of rostrum. *Phoberus* A. M. Edw.; *Nephropsis* W.-Mason, deep sea, with eyes reduced or 0; *Enoplometopus* M. Edw.

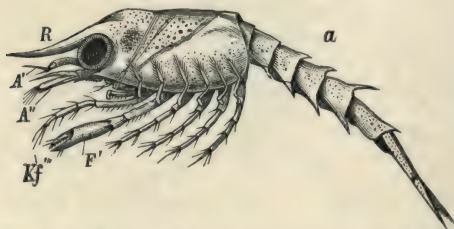


FIG. 327.—Young form (larva) of the lobster in mysis stage. A', A'' antennae; F' anterior ambulatory leg; Kf''' third maxilliped; R rostrum. (From Claus, after G. O. Sars.)

Sub-fam. 2. **Thaumastocheilinae.** A flattened rostrum; 1st trunk-legs chelate and unequal, 2nd chelate; gills filamentous. *Thaumastocheilus* Wood-Mason. 2nd antenna with scaphocerite. *T. zaleucus* W.-Suhm, has a right 1st chela with enormously elongated comb-like divisions, and is blind. Taken by the *Challenger*

from 450 fths. on *Globigerina* ooze.

Sub-fam. 3. **Potamobiinae.** The fresh-water Crayfishes of the N. Hemisphere. Carapace and uropods as above, but with the last thoracic segment movable on its predecessor. The epipodial plate of the first maxilliped without a branchia, but those of the 2nd–7th thoracic feet with this plate plaited and bearing gill filaments on its outer surface. Abdominal feet small, but all usually present, the 2 anterior pairs being modified in the male. *Astacus* M. Edw. (*Potamobia* Leach). Britain to Japan, and N. America west of Rocky Mts. The Crayfish of English streams, commonly called *Astacus fluviatilis* is, according to Faxon, *A. pallipes* Lereboullet. *Cambarus* Erichson, pleurobranchia absent from last thoracic segment. The crayfishes of N. America, east of the Rocky Mts., including the blind *C. pellucidus* (Tellkamp) of the Mammoth Cave of Kentucky.

Sub-fam. 4. **Parastacinae.** The fresh-water Crayfishes of S. Hemisphere. Epipodites of thoracic limbs not produced into a lamina, except the first in which it bears gill filaments. Swimmerets absent from the first abdominal segment, large in the succeeding segments. *Astacoides* Guérin, Madagascar; *Parastacus* Huxley, Brazil; *Paranephrops* White, N. Zealand; *Astacopsis* Huxley (including *Chaeraps* Erichson) and *Engaeus* Erichson, Australia.

Section 3. ANOMURA.

A group near the border line between the Macrura and Brachyura with great variety of form. In many the carapace is broad. The trunk-legs of the last pair are weak and not used in locomotion or for the prehension of food (Fig. 315, *Th.* 8). The sternum of the segment that bears them is free. The abdomen is usually bent under the thorax, and except in the Thalassinidea and Galatheidea, reduced. The 6th abdominal feet (uropods) are often broad and natatory in these two tribes. In the others they are reduced, and, in the Paguridea adapted for retaining

the animal in the shell it inhabits. They are only absent in the Lithodidae. In the Anomura the anterior part of the pleural fold of the carapace (pterygostomial region) is divided from the rest by a pleural suture, and projects freely in front, a notch, which receives the base of the 2nd antenna, separating it from the frontal border (Fig. 315). Rostrum not united by a ridge with the front of the epistome. Scaphocerite of 2nd antennae often present. Third maxillipeds usually narrow. The larvae hatch in the zoea form, with 2 pairs of maxillipeds (brachyuran character) and pass from this into a metazoea stage, in which the 3rd maxilliped is a functional swimming appendage, but the trunk-limbs are not biramous (the mysis stage being almost obliterated from the life-history).

The differentiating characters of the tribes of the Anomura are given by Borradaile as follows.

I. End-segments of 2nd-4th trunk-legs curved and flattened. 1st pair styliform or sub-chelate. Tail fin not adapted for swimming. Abdomen bent under thorax. Rostrum small or wanting. 3rd maxillipeds without mastigobranchs. *Hippidea*.

II. End-segments of 2nd-4th trunk-legs not curved or flattened. 1st pair not styliform, rarely sub-chelate.

1. 6th abdominal leg adapted for swimming (except in *Thalassinina*, where it is styliform). Abdomen symmetrical with the pleura usually well developed.

a. Body depressed. A pleurobranch to the last trunk-leg. Often a transverse suture on the telson. Abdomen more or less bent under the thorax. *Galatheidae*.

b. Body compressed. No pleurobranch to the last leg. No transverse suture on telson. Abdomen straight. *Thalassinidea*.

2. 6th abdominal limb, when present, adapted for holding the body in a shell or other covering, not for swimming. Abdomen nearly always asymmetrical, soft and twisted, or bent under the thorax. *Paguridea*.

Tribe 1. THALASSINIDEA.

Crustacea of moderate size, burrowing in sand and mud, at various depths, from the sea level to 500 faths. The last thoracic segment free and articulated with the preceding and often not covered by the hinder margin of the carapace. In all except the Axiidae a linea thalassinica (cf. p. 514) separates the median from the lateral region of the carapace. The segments of the long and often soft abdomen scarcely imbricated and

with reduced pleura. Eye stalks short, 1st pair of trunk-legs powerful, ending in chelae of which one is larger than the other, 3rd pair never chelate, the last pair directed backwards; uropods usually large. Branchiae often reduced in number, filamentous, and in some cases, foliaceous. An *appendix interna* usually present on the abdominal endopodites. The larvae hatch as zoeae (except *Eiconaxius* q.v.) and pass through a mysis stage, having, in accordance with the adult structure, an intermediate character between the zoeae larvae of the Caridea and the Anomura. Some superficial resemblances between the adults and the Stomatopoda are interesting from the similarity in the mode of life of the two groups. They have been divided into four families, which are however closely related. These are differentiated as follows.*

I. Fam. 1. **Axiidae**. No *linea thalassinica*. Both movable (scaphocerite) and fixed thorns† of 2nd antennae present, though sometimes minute (? 0 in *Scytoleptus*). Abdominal pleura large. *Axius* Leach. Scaphocerite scale-like. *A. stirhynchus* Leach. British and French coasts. In the sub-gen. *Eiconaxius*, from deep water in the Pacific, Spence Bate found that the young in the egg had all the limbs of the adult, except the first abdominal, the 3 last trunk-legs being biramous; *Axiopsis* Bor.; *Calocaris* Bell, last thoracic segment covered by the carapace, scaphocerite may be much reduced. Chelae not markedly unequal. Deep water forms. The eyes are developed, but the pigment is reduced or 0. *C. macandreae* Bell, Great Britain, Ireland, Norway. The zoeae larva has well developed eyes, and 3 swimming maxillipeds, as in Caridea (G. O. Sars). *Scytoleptus* Gerst.

II. *Linea thalassinica* present (except *Callianidea*). Fixed antennal thorn wanting. Scaphocerite reduced to a flattened vestige or 0. Abdominal pleura usually small.

(1) Fam. 2. **Laomedidae**. Sutures on both endopodite and exopodite of uropods. Abdominal pleura of good size. *Laomedea* de Haan; *Jaxea* Nardo; *Naushonia* Kingsley.

(2) No sutures on the last limb. Abdominal pleura small.

(a) Fam. 3. **Callianassidae**. Carapace laterally compressed; rostrum minute or 0. Scaphocerite vestigial. Second trunk-leg chelate or simple. Gills filamentous. No podobranchs on trunk-legs; abdom. legs 3-6 broad, uropods without suture. *Callianassa* Leach. swimmerets 3-5 broad and large. Some 18 spp. *C. subterranea* (Montagu), British. *Glypturus* Stimps. *Callianidea* M. Edw. swimmerets 2-5 very large and fringed with silky, articulated hairs. Western Pacific. *Upogebia* Leach (*Gebia* Auct.), 1st trunk-legs subequal and subchelate, swimmerets 2-5 large. *U. stellata* (Montagu), S. Devon, *U. littoralis* Risso, Mediterranean and Norway. Development studied by Sars who finds that the 3rd maxilliped is not present as a swimming appendage in the zoeae stage. *Gebicula* Alc.; *Bigea* Nardo.

(b) Fam. 4. **Thalassinidae**. Carapace dorsally flattened, with rostrum; scaphocerite 0; 1st and 2nd trunk-legs subchelate; abdominal appendages including uropods slender; branchiae filamentous and foliaceous; podobranchs on trunk-legs 1-3. *Thalassina* Latr. *T. scorpionoides* Latr. Pacific. 9 in. long.

* Cf. Borradaile, Classification of Thalassinidea. *A. and M. N. H.*, 7, vol. 12 (1903), p. 534.

† The *fixed thorn* is an external process from the 2nd segment of the antenna.

Tribe 2. **PAGURIDEA.**

The great majority of the hermit or soldier crabs and their allies are characterized by the possession of a soft and spirally twisted abdomen, which is protected by a Gasteropod shell or some other covering. With the spiral form of the abdomen is associated a loss of bilateral symmetry (the 2nd-5th appendages of the right, or concave side being aborted) like that which has befallen the Gasteropods whose shells these Crustacea inhabit. The carapace is elongated, becoming membranous behind the cervical groove. The sternal plastra are linear. Antenna 2 with a thorn-like scaphocerite ("acicle"). 1st trunk-legs with large unequal chelae, one (or both) of which acts as an operculum when the animal is withdrawn into its shell. The hindmost pairs short, warted, and, like the uropods, adapted for holding on to the interior of the shell. Gills phyllobranchiae or trichobranchiae. The eggs are hatched as zoea larvae. After the adult form is reached the shell in which the posterior region is sheltered is, of course, repeatedly changed to accommodate the growing body.

With the typical unsymmetrical hermit-crabs are associated the Pylochelidae, symmetrical forms which inhabit hollows in stones, worm tubes, sponges, etc., in deep water, the remarkable air-breathing *Birgus latro*, a Pagurid adapted to terrestrial life, and the Lithodidae which appear to have once acquired and since abandoned the pagurid habit.

Fam. 1. **Pylochelidae.** Abdomen symmetrical, with normal terga. Gills trichobranchiae. Two posterior trunk-legs modified as indicated above. Deep water. *Pylocheles* and *Mixtopagurus* A. M.-E. and *Chiroplatea* Sp. B. which is blind. *Pylocheles Agassizii* A. M.-E. was obtained by the Blake at 200 faths. off Barbados, in hollows in agglutinated sand. *P. spinosus* Henderson. Challenger. 150 faths. Australia.

Fam. 2. **Paguridae.** 2nd antenna with a well developed spine in place of the scale (Fig. 328).

Sub-fam. 1. **Eupagurinae.** 3rd maxillipeds separated at their bases

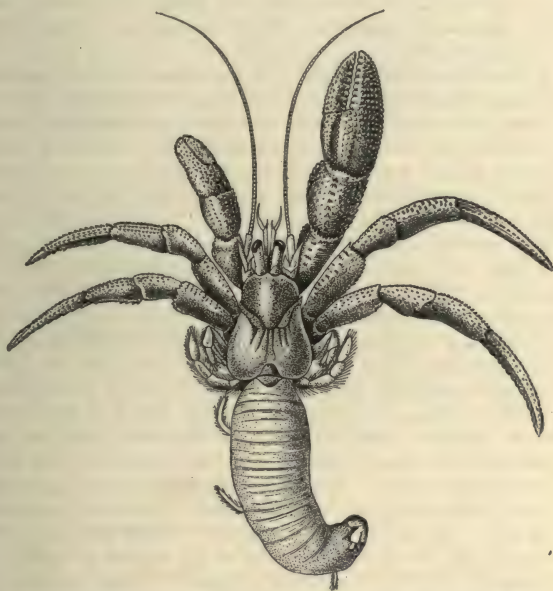


FIG. 328.—*Eupagurus (Pagurus) bernhardus* (from Claus, after Cuvier)

Parapagurus and *Sympagurus* S. J. Smith, deep sea. *Parapagurus* is said to have the opening of the oviduct on the left side only. *P. abyssorum* A. M.-E. below 1,000 faths. in the great oceans. It at first inhabits a shell (that of the pelagic *Ianthina*, or littoral shells are used) which is subsequently absorbed by an anemone (? *Epizoanthus*) which settles on it, and forms a covering which grows with the growth of the Pagurid. *Eupagurus* Brandt, many species, mainly littoral. *E. prideauxii* Leach, associated with the sea-anemone *Adamsia palliata*, which lives on the outside of the shell inhabited by the Pagurid. *Nematopagurus* A. M.-E and Bouv. *Spiropagurus* Stps. *Anapagurus*, Hend.

Sub-fam. 2. **Pagurinae.** 3rd maxillipeds approximated at their bases. *Pagurus* Fabr. In tropical seas. *Petrochirus* Stps.; *Calcinus*, *Clibanarius*, *Diogenes* and *Paguristes* Dana. A form named *Xylopagurus* A. M.-Edw., 100–200 faths., W. Indies, inhabits cylindrical pieces of wood, the end of the abdomen modified into a posterior operculum.

Fam. 3. **Cenobitidae.** 1st antennae with elongated and twice bent basal segments, and one of the flagella enlarged; 2nd compressed at the base. Gills foliaceous. *Cenobita* Latr., abdomen soft, unsymmetrical, with 2nd–4th appendages of left side in female, 0 in male; paired 6th appendage, larger on left side, in both sexes. Semi-terrestrial hermit-crabs. They wear Gastropod shells, and some species (the large red *C. perlatus* and *C. rugosus*) are able to produce a “low chirping sound” (Borradaile). The species are widely distributed in the Indo-Pacific region. *Birgus* Leach. *B. latro* (L.) an air-breathing Pagurid of large size sheltering in holes and fissures in the ground. Carapace completely calcified; abdomen symmetrical, broad, with calcified tergal plates, its appendages as in *Cenobita*. First trunk-legs bear very powerful chelae, the fourth small chelae. The postero-lateral regions of the carapace are expanded into large pulmonary chambers (Fig. 329), of which the 14 pairs of reduced gills occupy a small part. The upper and outer lining of the chambers is produced into ramified vascular tufts, abundantly supplied with blood-vessels, the efferent vessels falling into the branchial vein before it enters the pericardial sinus.* The surface is kept moist with sea-water which the animals repair to the shore to renew. They feed, among other substances, on the “meat” of the cocoa-nut † (they are hence known as robber crabs) and carry a rich store of oil in the abdomen. *Birgus latro* is probably to be regarded as a Pagurid whose ancestors were marine and wore shells, but which has taken to a terrestrial life.

The statement that the young of *Birgus latro* are hatched with the same form as the parents has been shown to be incorrect. Like those of other Pagurids they hatch as zoeae larvae. A female of this species was observed by Dr. A. Willey, at Lifu, in the Loyalty Islands, at the edge of the sea, with the abdomen covered with just hatched zoeae which were being washed off to start their free-swimming larval life. The zoeae larvae of *Coenobita* have also been observed, by Borradaile.‡

* Semper, *Animal Life*, 3rd edition, p. 193.

† Darwin, *Naturalist's Voyage*, p. 462.

‡ Borradaile, L. A. On the young of the Robber-Crab (*Birgus latro*), *Willey's Zoological Results*, part V, p. 585. Camb. Univ. Press, 1900, and Note on the Hatching-stage of the Pagurine Land-crabs, *Proc. Zool. Soc.*, 1899, p. 937.

Fam. 4. **Lithodidae.** Carapace broadly ovate, uneven, with prominent rostrum; 1st antennae with cylindrical peduncles and 2 short flagella; 2nd with an acicle; 1st trunk-legs chelate, 5th slender, chelate, folded in the branchial chambers. Abdomen bent under thorax, without uropods, 3-5 terga represented by paired lateral plates, with the appendages only present in the female, and unsymmetrically developed. Inhabit shallow water of the arctic or antarctic zones, and the intermediate

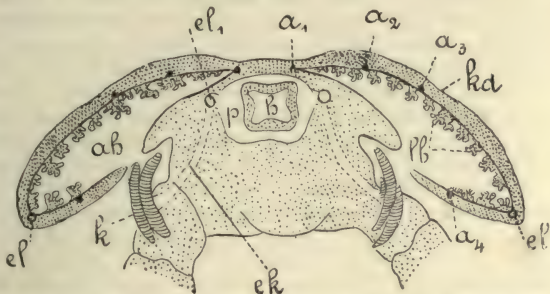


FIG. 329.—*Birgus latro*. Diagrammatic transverse section in the region of the heart. *a*₁–*a*₄ pulmonary or shell vessels leading from the heart; *ah* respiratory chamber; *ek* brachial blood-canals leading to the heart; *el* pulmonary vessels leading to the heart; *el*₁ the same near the entrance into the pericardium; *h* heart; *k* brachiae; *kd* branchiostegite; *lb* respiratory tufts; *p* pericardium. (From Lang, after Semper.)

cold, deep water in temperate and tropical regions, though some are littoral. They are regarded as derived from the Pagurid stock, having partially regained their bilateral symmetry, and acquired a crab-like appearance. The larva of *Lithodes* hatches in metazoea form.

Sub-fam. 1. **Hapalogastrinae** (= Hapalogastrica Brandt). *Hapalogastr* and *Dermaturus* Brandt; *Placetron* Schalfew.

Sub-fam. 2. **Ostracogastrinae.** *Phyllolithodes* Brandt; *Neolithodes* M.-E. and Bouv.; *Paralithodes* Brandt; *Lithodes* Latr., robust and covered with spines. Some spp. British. Widely distributed in deep water, and littoral. *Acantholithus* Stps.; *Palalomis* White; *Rhinolithodes* Brandt; *Echidnocerus* White; *Cryptolithodes* Brandt.

Tribe 3. GALATHEIDEA.

Body symmetrical, depressed. Abdomen well developed usually ventrally flexed, but not, except in the Porcellanidae, applied to the sterna of the thorax, with uropods. Rostrum usually well developed. 3rd maxillipeds 7-segmented, leg-like or with the basal segments expanded. The 1st trunk-legs alone carry regular chelae, the 5th slender and folded in the branchial chamber. Gills usually phyllobranchiate (trichobranchiate in *Aeglea*). Generative orifices on coxae. *Aeglea* is the only fresh-water genus, the others are littoral or deep sea.

Fam. 1. **Aegliidae**: Gills trichobranchiate. Eight arthrobranchiae and 3 rudimentary pleurobranchiae. 2nd antennae without a scale. *Aeglea* Leach. The sole sp. *A. laevis* Lat. in mountain streams in S. America.

Fam. 2. **Chirostylidae.** Gills as in the remaining families, i.e. phyllobranchiate: 7 arthrobranchiae and 4 pleurobranchiae. Ant. 2 with spine-like scale. *Chirostylus* Ortm., trunk-legs very long. *Uroptychus* Hend.; *Eumunida* Smith.

Fam. 3. **Galatheidæ.** Rostrum well developed, triangular or spine-

like. Scale of 2nd antenna rudimentary or 0. Abdomen ventrally flexed, but not folded against the sternum. Littoral and deep sea.

Sub-fam. 1. **Galatheinae**. Eyes well developed. Exopodite of 1st maxilliped ending in a flagellum. *Galathea* Fabr. Eye-stalk little or not at all widened distally, rostrum triangular. Thirty littoral spp., some British. *Munida* Leach. Eye-stalk widened distally, rostrum spine-like. Thirty spp. littoral to deep sea. *M. Rondeletii* (Fig. 315), British. 1st trunk-legs very long. *Pleuroncodes* Stps.

Sub-fam. 2. **Munidopsinae**. Eyes reduced. Exopodite of 1st maxilliped without a flagellum. Deep sea. *Galacantha* A. M.-E.; *Munidopsis* Whiteaves; *Galathodes* A. M.-E.; *Elasmonotus* A. M.-E.

Fam. 4. **Porcellanidae**. Rostrum short and broad or 0. Scale of 2nd antenna 0. Abdomen bent and applied to thorax as in Brachyura, but with a small swimming fan. Some 6 genera, all littoral; under stones between tide marks. *Petrolisthes* Stimps.; *Pachycheles* Stimps. 11 spp. chiefly tropical. *Porcellana* Lmk. Cephalo-thorax longer than broad; larva with very long rostral and posterolateral spines. 20 or 30 spp. widely distributed. *P. platycheles* (Pennant) and *P. longicornis* (L.) common under stones round our shores. *Megalobrachium* Stps. and *Polyonyx* Stps. live a semi-parasitic life in sponges, the mollusc *Aspergillum*, etc. Warm seas. *Raphidopus* Stps.

Tribe 4. HIPPIDEA.

Shallow-water forms living buried in sand. The body is nearly cylindrical, and the abdomen is loosely folded under the thorax. Other characters are noted above (p. 537).

Fam. 1. **Hippidae**. Sand crabs. Carapace ovate or subquadrate, overlapping the bases of the legs; thoracic sterna linear; eyes with small corneae; 1st antenna with 1 long flagellum; 2nd with massive base; 3rd maxillipeds suboperculiform, without exopodite; 1st trunk-legs not chelate, 5th filiform; abdomen partly extended, with long lanceolate telson, 6th appendages large and lamellar, adapted not for swimming but for digging as the animal buries itself, backwards, in the sand. *Hippa* hatches as a zoea with 2 pairs of maxillipeds, and very long rostrum. *Hippa* Fabr. 2nd antennae with long curved flagella, mandibles functionless, and fused with the adjacent parts of the shell; first abdominal segment fused with thorax. *H. eremita* (L.) live in great numbers on sandy shores of the eastern United States, near low tide level, and burrow with great rapidity. They apparently live, after the manner of earthworms, on the organic matter contained in the sand, which they swallow in large quantities (Smith). *Remipes* Latr. 2nd antenna with short flagellum. *Mastigochirus* Miers, first trunk-legs flagelliform.

Fam. 2. **Albuneidae**. Resemble the last family, but 3rd maxillipeds are subpediform, with exopodite, and first trunk-legs are chelate; carapace flattened, but not overlapping the bases of the legs, excavated for reception of 1st abdominal segment; telson ovate. *Albunea* Fabr. Mediterranean, Celebes, first antennae form, when in apposition, a channel for the respiratory water. *Blepharipoda* Randall.

Section 4. BRACHYURA.

The carapace is broad and longer than the short abdomen. The latter is without a caudal fin, is bent forwards and applied to

the broad thoracic sterna. Pterygostomial region fused in front with the epistome, and not separated by a movable suture from the rest of the carapace. A median ridge unites the epistome with the rostral region of the carapace. The eyes and first antennae are received in pits of the cephalo-thorax. The second antennae project on the inner side of the eye stalks. Both pairs bear short flagella. The endopodite of the first maxilliped is broad, unjointed and terminates in a well marked outer angle. The third maxillipeds are broad and opercular. The first trunk-legs alone are chelate. The abdomen is narrow in the male and bears only the one or two anterior appendages (copulatory); wide in the female, with 4 ovigerous fan-like appendages; but the sixth pair (uropods) is never present. The gills are phyllobranchiate. In nearly all cases the eggs hatch as zoea larvae, with the two pairs of biramous swimming maxillipeds, and long spines (dorsal, frontal and paired lateral). A *metazoea* and *megalopa* stage are passed through, but a mysis stage is absent from the life-history.

Tribe 1. BRACHYURA ANOMALA.

Fourth and fifth trunk-legs articulated higher than their predecessors; epistome * broad; as many as 14 pairs of gills may be present and the openings of the oviducts are on the bases of the third trunk legs, not on the adjacent sterna. In these two features the members of this family differ from the other Brachyura and resemble the Macrura, with which group they are often classified.

Fam. 1. **Homolidae.** Eye-stalks long and usually slender; orbits and fossae for first antennae incomplete or absent; last pair of legs small, and prehensile. Tropical and subtropical, down to 825 faths. *Dicranodromia* A. M. Edw., intermediate between this and the next sub-family, but with incomplete orbits and no fossae for 1st antennae. *Homola* Leach, carapace quadrilateral; 14 pairs of gills. 3rd maxilliped leg-like. *Latreillia* Roux, carapace triangular, legs slender and cylindrical with a superficial resemblance to spider-crabs.

Fam. 2. **Dromidae.** Carapace usually sub-globular; orbits well defined; 5th and usually 4th trunk-legs short, prehensile and used for carrying a shell, sponge, ascidian colony or other sheltering object over the back; 14 pairs of gills. *Dromia* Fabr. carapace pilose. *D. vulgaris* M. Edw. Mediterranean, sometimes British, with a strange shaggy aspect; regarded as "poisonous and narcotic," by the ancients; male copulatory organs large. *Petalomera* Miers; *Dynomene* Latr. only the 5th legs sub-dorsal.

* The epistome is, as stated above, the region between the front of the carapace and the anterior border of the mouth; the latter being well marked in the Brachyura. The terms *broad* and *narrow* in the following descriptions apply to the antero-posterior dimensions of the epistome.

Tribe 2. OXYSTOMATA.

Carapace usually convex; buccal frame triangular, the mouth cavity being prolonged on either side to the front as two convergent efferent respiratory channels containing the grooved ends of the endopodites of the first maxillipeds; the afferent openings often conspicuous, in front of the bases of the chelipeds (except Leucosiidae, q.v.). Their habit is to lie buried in sand, with the tip of the rostrum alone uncovered.

Fam. 1. **Dorippidae**. Carapace truncated in front; the last or last two pairs of legs short, feeble, semi-prehensile and situated dorsally, as in the *Brachyura Anomala*. *Dorippe* Fabr. *Ethusa* Roux, carapace longer than broad, approaching the *Macrura*; from moderate depths to nearly 2,000 faths.

Fam. 2. **Leucosiidae**. Afferent respiratory channels open, not behind the pterygostomial regions, as usual, and as in other families of this group, but at the antero-lateral angles of the buccal frame, whence a channel leads to the base of the 3rd maxilliped. 2nd antennae much reduced. *Leucosia* Fabr. carapace smooth, semi-globose and produced anteriorly, with a pit (? nonrespiratory) in front of the bases of the chelipeds. Often polished and beautifully coloured. *Philyra* Leach. *Myra* Leach. *Ebalia* Leach, carapace sub-orbiculate, uneven. Littoral and deeper waters, Atlantic and Indo-Pacific. Four British spp. *Ixa* Leach; *Oreophorus* Rüppell. *Acanthocarpus* Stimpson, a specimen, dredged by the *Blake* from deep water, has a stridulating apparatus on the chela and carapace.

Fam. 3. **Calappidae**. Carapace convex, sometimes orbicular; the terminal joints of 3rd maxillipeds not concealed by the 4th joint. *Calappa* Fabr. the carapace with the large crested chelipeds form together a ball-like whole, the postero-lateral margins prolonged over the other trunk-legs. Littoral forms of warm seas. *Paracyclois* Miers; *Cryptosoma* Brullé; *Platymera* M. Edw. *Orithyia* Fabr. the 4 posterior pairs of legs flattened for swimming.

Fam. 4. **Matutidae**. Terminal segments of 3rd maxillipeds concealed by 4th segment. *Matuta* Fabr. 4 posterior pairs of legs flattened, but not setose. They burrow in sand. *Hepatus*, Latr., *Osachila* Stimpson, and *Actaeomorpha*, Miers, have claw-like ends to the legs.

Fam. 5. **Raninidae**. Carapace ob-ovate or ovate oblong, the short abdomen partially extended, not folded under the thorax; 1st antennae not folded in special fossae; the 4 posterior pairs of trunk-legs with broad terminal joints. Tropical and sub-tropical waters, down to 300 faths. *Ranina* Lam. carapace broad and truncated in front. Afferent branchial opening at posterior end of thorax. Only 9 pairs of gills. Male copulatory appendages large. East Indies and Pacific Islands. *Raninoides* M. Edw. last pair of legs filiform; *Notopus* de Haan, *Lyreidus* de Haan. *Zanclefer* Henderson, with short legs with sickle-shaped end-joints, W. Atlantic coasts. In these two genera the orbits are ill-defined.

Tribe 3. OXYRHYNCHA.

Carapace narrowed in front, usually rostrate; buccal frame quadrate, and epistome large. Central nervous system attains its maximum of concentration. Many of the Oxyrhyncha have serrated and hooked hairs on the upper surface, which serve the purpose of holding fragments of algae, sponges, *Acyonium* colonies and other organisms with which they deck themselves, and which grow in this position. They dress in accord-

ance with their environment, and a crab dressed in algae has been observed to pick them off when placed in an aquarium with sponges, replacing them with portions of the latter (Graeffe, Eisig, Sluiter, Robertson, Aurivillius).

I. Basal antennal segment well developed, usually occupying a great part of the infra-ocular space.

Fam. 1. **Inachidae**. Eyes not retractile, or retractile against the sides of the carapace; orbits in general not defined. Rostrum simple or bifid, walking legs sometimes very long. *Macropodia* Leach (= *Stenorhynchus* Lam.) Spider Crab. *M. rostratus* (L.) and *M. longirostris* (Fabr.)

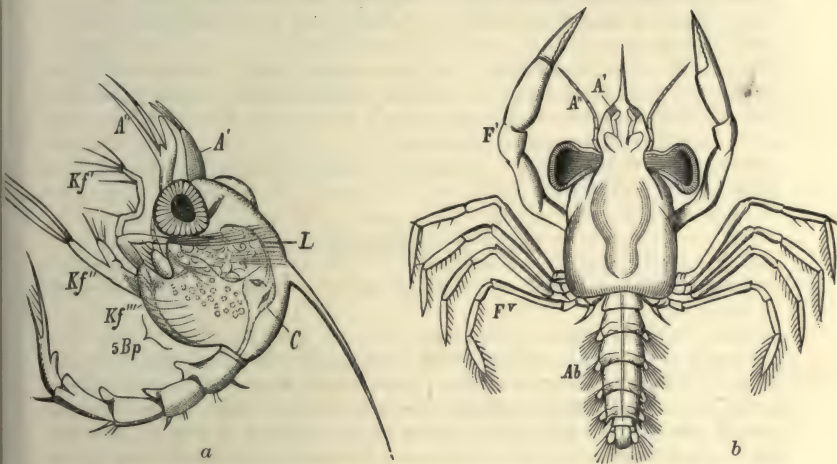


FIG. 330.—a, Zoaea of *Inachus* in advanced stage with rudiments of the third maxilliped (*Kf'''*) and the five pairs of ambulatory feet (*sBp*); *C* heart; *L* liver. b, *Megalopa* stage of *Portunus*; *Ab* abdomen. *F'* to *Fv* first to fifth ambulatory legs.

are common in depths of a few fathoms round our coasts. *Achaeus* Leach. *A. Cranchii* Leach. British. *Inachus* Fabr., cephalothorax triangular, spiny, rostrum short, chelipeds much shorter than the succeeding pair of legs. In this, as in other genera which are infested with parasitic Crustacea (Isopods, Cirripeds, etc.) the males so circumstanced may assume hermaphrodite characters (see p. 415). *I. dorsetensis* (Penn.), *I. dorynchus* Leach and *I. leptochirus* Leach, are British. *Leptopodia* Leach, rostrum not bifid, but long and serrated. *Macrocheira* de Haan. *M. Kämpferi* de Haan has a span of 8–11 feet. *Huenia* de Haan. *Lispognathus* A. M. Edw. *L. thomsoni* (Norman) widely distributed, has been taken at depths down to 600 faths. *Ergasticus* A. M.-Edw. *Platymaia*, *Cyrtomaia* and *Echinoplax* Miers. *Euprognatha* Stimpson.

Fam. 2. **Maïidae**. Eyes retractile within orbits, whose margins are fissured. *Maia*, Lam. cephalothorax round-ovoid, with projecting deeply cleft rostrum; basal joint of 2nd antenna with 2 long spines. *M. squinado* Herbst, legs rather short, shell spiny. Mediterranean, extends to S. coast of England. *M. verrucosa* M.-Edw. *Hyas* Leach, cephalothorax oval, somewhat flattened, with pointed rostrum and without a preorbital spine. *H. araneus* (L.) and *H. coarctatus* Leach. British. *Chorinus* Latr

Arctopis, Lam. (*Pisa*, Leach) cephalothorax elongated pear-shaped with preorbital spine and long rostrum, basal joint of 2nd antenna narrow and inserted besides the rostrum; two spp. British. *Lissa* Leach. *Chionocetes* Kröy. Greenland and New England, spans 32 inches. *Antilibinia* MacL. *A. Smithii* M'Leay, has powerful claws with which it clings to wave-beaten rocks. Natal. *Scyramathia* M. Edw. *Eurynome* Leach, cephalothorax irregularly rhomboid. *E. aspera* (Penn.) Mediterranean, extending to Britain.

Fam. 3. **Periceridae**. Eyes retractile within complete orbits. *Pericera* Latr., *Macrocoeloma* Miers, *Libinia* Leach. *Mithrax* Latr.

II. Basal antennal segment very small, the orbit having an inferior wall distinct from it.

Fam. 4. **Parthenopidae**. Chelipeds very long. *Paranthope* Fabr. *P. horrida* (L.) the great warty crab of the E. and W. Indies; *Lambrus* Leach, cephalo-thorax triangular; widely distributed in the shallow water of warm seas; *Heterocrypta* Stimpson.

With the Oxyrhyncha is probably allied *Paratymolus* Miers, from Australia.

Tribe 4. CATOMETOPA.

Carapace broad anteriorly, not rostrate, the *front** bent downwards, epistome short.

Fam. 1. **Grapsidae**. Carapace more or less quadrilateral; front generally very broad; mostly littoral or shallow water forms. *Grapsus* Lam. Carapace with transverse ridges; some species frequent exposed rocks, running with great agility. *Nautilograpsus* M. Edw. *N. minutus* (L.) widely distributed and abundant in the Gulf-weed of the N. Atlantic. Like other members of the Gulf-weed fauna it is mottled with yellow, brown and white in varying patterns, resembling the young and old branches of the weed, with the white encrusting Polyzoan colonies which grow on it. Several members of this, as of the two succeeding families, have adopted a semi-terrestrial mode of life. *Eriocheir* de Haan; *E. japonicus* de Haan, with furry chelae, ascends fresh-water streams in Japan, and lives partly on land. *Sesarma* Say, widely distributed in warm, shallow waters. *S. pisonii* climbs mangrove bushes, taking air into its branchial cavity by openings at the back of the thorax. Another species inhabits marshy ground and has a sieve-like arrangement of hairs on the pterygostomial region for re-aerating the water driven from the branchial cavity, and conducting it to the afferent opening in front of the bases of the chelipeds. It is also able to take in air at the back of the thorax (Fr. Müller). Several other genera.

Fam. 2. **Ocypodidae**. Carapace moderately convex, sometimes trapezoidal; front of moderate width or very narrow. Eye-stalks may be greatly developed; terminal joints of walking legs styloform, without strong spines. Littoral to considerable depths. *Ocypode* Fabr. front narrow, orbits and eye-stalks very large, the latter often prolonged beyond the (lateral) corneal surface. Chelae unequal in male, the larger one very mobile, the 6th joint ("hand") bearing a regularly striated band which plays over a ridge on the third joint, forming a stridulating apparatus.

* The "front" is the region of the upper surface of the carapace between the orbits.

They burrow between tide marks, and, as the name implies, are very swift of foot. Running on tip-toe, with the long eye-stalks erect, "on wind-swept stretches of sandy beach, and coloured like the sand, they sometimes seem rather to be borne on the wings of the wind than to run" (Stebbing). They take air into the branchial cavity, and are unable to survive a prolonged immersion in water (Fr. Müller); afferent orifice between the bases of 4th and 5th walking legs, guarded by fringes of hairs. *Gelasimus* Latr. One of the chelae (r. or l.) very large in the male. They live, in pairs, in burrows, on sandy shores in the tropics, often in great numbers, and between tides come out and feed. The great chela of the male is brightly and variously coloured, giving the stretches of sand they frequent the appearance of being strewn with coloured beans. It is held aloft and brandished, in defiance, at the neighbouring males, who simultaneously respond with a similar motion. Sometimes an engagement occurs, the males grasping hands. If they are disturbed there is a flash of the great chelae as the crabs retreat to their burrows and in a moment the shore is deserted. They live on vegetable matter in the sand, and (in Tongatabu) are eaten by king-fishers. *Gonoplax* Leach, chelipeds very long in male; *G. rhomboides* (L.) British; many other genera. In *Macrophthalmus* Latr., *Helice* de Haan, and *Metaplex* M. Edw. the males are provided with stridulating apparatus. *Bathyplox* A. M. Edw. *B. typhlus* A. M. Edw. Specimens from 4-500 fathoms blind, while those from shallow water can see.

Fam. 3. **Gecarcinidae.** Land crabs. Carapace dorsally convex, dilated over the branchial regions, anterolateral margins entire; front of moderate width; terminal joint of walking legs armed with spines; Branchial chambers lined by spongy membrane, and only partially occupied by the gills. A supply of water is retained in them. *Uca* Leach, and *Gecarcinus* M. Edw. 3rd maxillipeds meet in the middle line. *Uca una* (L.) in mangrove swamps, Brazil. In *Cardisoma* Latr., *Gecarcoidea* M. Edw., *Gecarcinus* Leach and *Hylaeocarcinus* Wood-Mason, a lozenge-shaped space is left between these maxillipeds. A species of *Gecarcinus* inhabits the forests of the W. India Islands, sheltering in holes. In May they make their way in compact bodies, scaling the obstacles in their paths, to the sea, where the eggs are laid. "The noise of their march is compared to the rattling of the armour of a regiment." The young are hatched, according to Westwood, with the form of the adult. This is probably not the case in *G. lagostoma*, whose wide distribution would suggest that the larva leads a pelagic existence.

Fam. 4. **Pinnotheridae.** Carapace more or less membranous, anterolateral margins entire or nearly so; eyes very small. Small crabs, many of them living symbiotically with Lamellibranchs, *Echini*, etc. A crab associated with a *Pinna* appears on the Egyptian monuments. *Pinnotheres*, Latr., only 3 pairs of gills. *P. veterum* Bosc. and *P. pisum* (L.) are common European (British). The female of the latter is never found outside a host, and the carapace is much more membranous than in the male. *Hymenosoma* Desmarest; *Scopimera* de Haan; *Dotilla* Stimpson; *Pinnixa* White, 5th legs often short; *Amorphopus* Bell, 5th legs rudimentary; *Hexapus* de Haan, and *Thaumastoplax* Miers, 5th legs absent.

Here are probably allied the crabs which live in holes in Corals. In the male the abdomen has the usual shape, but in the female it is large and membranous, with expanded pleura, forming a deep pocket for the reception of the eggs. *Cryptochirus* Heller; *Haplocarcinus* Stimpson.

With the *Catometopa* is probably also allied *Cymopolia* Roux (= *Palicus*), Mediterranean and G. of Mexico.

Tribe 5. CYCLOMETOPA.

Carapace wide and regularly arched anteriorly; the front not depressed nor rostrate, epistome short.

Fam. 1. **Thelphusidae (Potamonidae)**. Carapace dilated over the branchial regions. Fluvial or in damp forests. Classed by some authors with the *Catometopa*, and intermediate between these and the *Canceridae*. *Thelphusa* Latr. *Th. fluviatilis* Latr. (*Potamon edule*) widely distributed, S. Europe, N. Africa. The young leave the egg in the adult form (Mercanti). *Th. dehaanii* White ascends to 2,500 ft. in Japan. *Paratelphusa* M. Edw. Indo-Malayan. *Deckenia* Hilg., E. Africa and Seychelles, has acquired an efferent respiratory channel similar to that of the *Oxystomata*.

Fam. 2. **Canceridae**. Carapace broad, convex, anterior margins arched; front moderately wide. Some 50 genera. *Cancer* L. front 3-toothed; *C. pagurus* L. the crab of the markets, frequents holes in rocks, in pairs. *Pilumnus* Leach. *P. hirtellus* (L.) British; front projecting, cephalo-thorax high arched. *Pirimela* Leach, *P. denticulata* (Montagu) British. *Eriphia*, Latr.

Fam. 3. **Trapeziidae (Xanthidae)**. Carapace depressed and nearly quadrilateral, antero-lateral margins entire or with 1 tooth. Small crabs of warm seas. Spp. numerous in the tropics. *Trapezia*, Latr.; *Tetralia* and *Quadrella*, Dana. *Xantho* Leach. *X. incisus* Leach, and *X. hydrophilus* (Herbst) British. *Pseudozoeus*, Dana. *Ps. bouvieri* A. M.-Edw. has a stridulating apparatus in which vibrations are produced by a ridge on the 5th segment of the chelipeds, playing over the striated antero-lateral margins of the carapace. *Melia* Latr. *M. tessellata*, frequents coral and has the remarkable habit of carrying a live sea-anemone in the chela.*

Fam. 4. **Portunidae**. Carapace depressed, usually widest at the last antero-lateral spine. 5-9 teeth on the antero-lateral margin; the 5th legs of the trunk usually flattened and adapted for swimming. *Carcinus* Leach. 7th segment of 5th legs narrowly lanceolate, antero-lateral margins of shell 5-toothed. *C. moenas* (Penn.) the common shore crab of the British Islands. *Portunus*, Fabr. Frontal border 5-toothed; last two segments of 5th legs flattened, the last joint ovate. *P. puber* (L.) the velvet crab, *P. depurator* (L.) and 6 other spp. are British. *Portumnus* Leach, 7th segment of 5th legs lanceolate. *P. variegatus* Leach, British. *Platyonichus* Latr. 7th segment of 5th legs broadly oval, good swimmers, as are spp. of *Polybius* Leach. *Scylla* de Haan, carapace very broad, with 9 or more teeth on the antero-lateral margin, and *Charybdis* de Haan, 7 or fewer teeth on the antero-lateral margin, are brilliantly coloured; *Bathynectes* Stimpson, *B. superbus* (Costa) N. Atlantic (including Mediterranean); *B. longipes* Risso, also British.

Fam. 5. **Podophthalmidae**. Carapace widest anteriorly, front narrow and spatuliform; with greatly elongated eye-stalks. *Podophthalmus* Lam. *Euphyllax* Stimpson.

Fam. 6. **Cyclidae**. Carapace orbiculate. *Acanthocycclus*, M. Edw. and Lucas, *A. Gayi* M. Edw. and Lucas. Chili and Patagonia.

* Cf. Borradaile. Gardiner's *Fauna and Geography of the Maldive and Laccadive Archipelagoes*, vol. i, p. 249.

Fam. 7. **Corystidae.** Sternal plastron narrow; 2nd antennae with long flagella; 3rd maxillipeds narrow, usually not operculiform. *Corystes* Latr., carapace longer than broad; *C. cassivelaunus* (Penn.). Markings on carapace resemble a human face; chelipeds very long in male; the long flagella of the 2nd antennae, applied together, form an afferent channel for the respiratory water, when the animal lies buried in sand; when it is not buried the current can be reversed; front rostrate in the young. Common on our shores, where it is often cast up by the sea. *Nautilocorystes* and *Pseudocorystes* M.-Edw. closely allied. *Atelecycclus* Leach, with operculiform 3rd maxillipeds, and *Thia* Leach are British. *Th. polita* Leach (= *residua* Herbst) with polished carapace and abdomen narrow in both sexes.

CHAPTER VI.

CLASS II. ONYCHOPHORA.*

Tracheates with a dermomuscular body-wall, paired segmental nephridia, and with numerous and similar pedigerous segments. The head is not marked off from the body and bears one pair of antennae, one pair of jaws and one pair of oral papillae. The tracheal stigmata are diffusely scattered and there are no malpighian tubes. Muscular fibres (excepting those of the jaws) unstriated.

* Balfour, F. M., The Anatomy and Development of *P. capensis*, Posthumous Memoir, edited by H. N. Moseley and A. Sedgwick, *Quart. J. Mic. Sci.* xxiii, 1883. Bouvier, E. L., *Monographie des Onychophores*, Paris, 1907 (*Ann. des Sci. Nat.* (9), 2 and 5). Dendy, A., On the Oviparous Species of Onychophora, *Q.J.M.S.* xlv, 1902, p. 362. Evans, R., On Onychophora from the Siamese Malay States, *Q.J.M.S.* xlv, 1901, p. 473, and On the Development of *Eoperipatus*, *ibid.* xlv, 1901, p. 1. Fletcher, J. J., On the Specific Identity of the Australian *Peripatus*, usually supposed to be *P. Leuckarti*, Saenger, *Proc. Linn. Soc. New South Wales*, x, 1895, p. 172. Gaffron, E., Beiträge z. Anat. u. Physiol. v. *Peripatus*, Th. 1 and 2, *Zool. Beiträge* (Schneider), i, pp. 33, 145. Guilding, L., *Mollusca caribbæana*: an account of a new genus of Mollusca, *Zool. Journal*, ii, 1826, p. 443, pl. 14; reprinted in *Isis*, xxi, 1828, p. 158, pl. ii. Moseley, H. N., On the Structure and Development of *Peripatus capensis*, *Phil. Trans.*, 1874. Pocock, R. J., Contributions to our knowledge of the Arthropod Fauna of the West Indies, Pt. 2, *Malacopoda*, &c., *Journ. Linn. Soc.* xxiv, p. 518. Purcell, W. F., On the South African Species of *Peripatus*, etc., *Annals of the South African Museum*, i, 1898-99, p. 331, and Anatomy of *Opisthopatus cinctipes*, *ibid.* ii, 1900. Selater, W. L., On the early Stages of the Development of a South American Species of *Peripatus*, *Quart. J. of Mic. Sci.* xxviii, 1888, pp. 343-361. Sedgwick, A., A Monograph of the Development of *Peripatus capensis* (originally published in various papers in the *Quart. J. Mic. Sci.* 1885-88); *Studies from the Morphological Lab. of the University of Cambridge*, iv, 1889, pp. 1-146; A Monograph of the Species and Distribution of the Genus *Peripatus*, Guilding, *Quart. J. Mic. Sci.* xxviii, 1888, pp. 431-494. Sheldon, L., On the Development of *Peripatus novæ zealandiæ*, Pts. 1 and 2, *Quart. J. Mic. Sci.* xxviii and xxix, 1888 and 1889. The memoirs quoted by Selater, Sedgwick and Sheldon, are all reprinted in vol. iv of the *Studies from the Morphological Lab. of the University of Cambridge*, vol. iv, 1889. Cambridge University Press. Steel, T., Observations on *Peripatus*, *Proc. Linn. Soc. New South Wales*, 1896, p. 94. Willey, A., The Anatomy and Development of *P. novæ britannicæ*, *Zoological Results*, Pt. 1, 1898, pp. 1-52, Cambridge. Sedgwick, On the Distribution and Classification of the Onychophora, *Q.J.M.S.* 1908.

The genus *Peripatus* was established in 1826 by Guilding, who first obtained specimens of it from St. Vincent in the Antilles. He regarded it as a Mollusc, being no doubt deceived by the slug-like appearance given by the antennae. Specimens were subsequently obtained from other parts of the neotropical region and from South Africa and Australia, and the animal was variously assigned by the zoologists of the day to the Annelida and Myriapoda. Its true place in the system, as a primitive member of the group Arthropoda, was first established in 1874 by Moseley, who discovered the tracheae.

There can be no doubt that *Peripatus* is an Arthropod, for it possesses the following features, all characteristic of that group, and all of first-class morphological importance : (1) The presence of appendages modified as jaws ; (2) the presence of paired lateral ostia perforating the wall of the heart and putting its cavity in communication with the pericardium ; (3) the presence of a vascular body cavity and pericardium (haemocoelic body cavity) ; (4) absence of a perivisceral section of the coelom. Finally, the tracheae, though not characteristic of all the classes of the Arthropoda, constitute a very important additional reason for uniting *Peripatus* with it.

Peripatus, though indubitably an Arthropod, differs in such important respects from all the old-established Arthropod classes, that a special class, equivalent in rank to the others, has had to be created for its sole occupancy. This unlikeness to other Arthropoda is mainly due to the annelidan affinities which it presents, but in part to the presence of the following peculiar features : (1) The number and diffusion of the tracheal apertures ; (2) the restriction of the jaws to a single pair ; (3) the disposition of the generative organs ; (4) the texture of the skin ; and (5) the simplicity and similarity of all the segments of the body behind the head.

The annelidan affinities are superficially indicated in so marked a manner by the thinness of the cuticle, the dermo-muscular body wall, the hollow appendages, that, as already stated, many of the earlier zoologists who examined *Peripatus* placed it amongst the segmented worms ; and the discovery that there is some solid morphological basis for this determination constitutes one of the most interesting points of the later work on the genus. The annelidan features are : (1) The paired

nephridia in every segment of the body behind the first two (Saenger, Balfour); (2) the presence of cilia in the generative tracts (Gaffron). It is true that neither of these features are absolutely distinctive of the Annelida, but when taken in conjunction with the annelidan disposition of the chief systems of organs, viz. the central nervous system, and the main vascular trunk or heart, they may be considered as indicating affinities in that direction. *Peripatus*, therefore, is zoologically of extreme interest from the fact that, though in the main arthropodan, it possesses features which are possessed by no other Arthropod, and which connect it to the group to which the Arthropoda are in the general plan of their organization most closely related. It stands absolutely alone as a kind of half-way animal between the Annelida and Arthropoda. There is very little gradation of

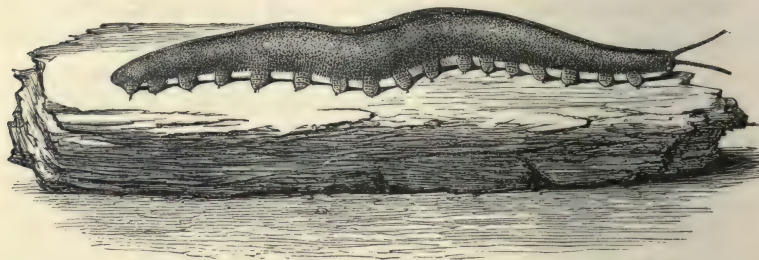


FIG. 331.—*Peripatus capensis*, drawn from life. Life size. (After Sedgwick.)

structure within the genus; the species are limited in number, and in all of them the peculiar features above mentioned are equally sharply marked.

Peripatus is a segmented animal, the segments being marked by the appendages. The ridges of the skin are considerably more numerous than the true segments. The number of segments is usually variable in the same species, but it is always complete at birth being definitely fixed at an early stage of development. The anterior part of the body may be called the head, though it is not sharply marked off from the rest of the body (Fig. 331). The head carries three pairs of appendages, a pair of simple eyes, and a ventrally placed mouth. The body is elongated and vermiform; it bears a number of paired appendages, each terminating in a pair of claws, and, except for the fact that the last pair or last two pairs are occasionally somewhat reduced, all closely alike. The number varies in the

different species. The anus is always at the posterior end of the body, and the generative opening is on the ventral surface just in front of the anus; it may be between the legs of the last or penultimate pair (Fig. 332), or it may be behind them. There is in most species a thin median white line extending the whole length of the dorsal surface of the body, on each side of which

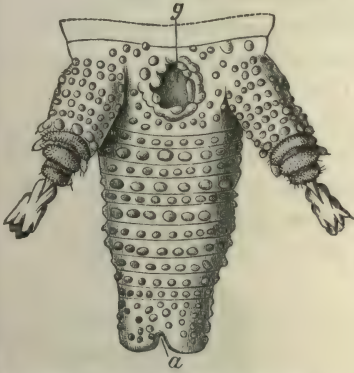


FIG. 332.—Ventral view of hind end of *P. novae-zealandiae* (after Sedgwick).
g generative opening; *a* anus.

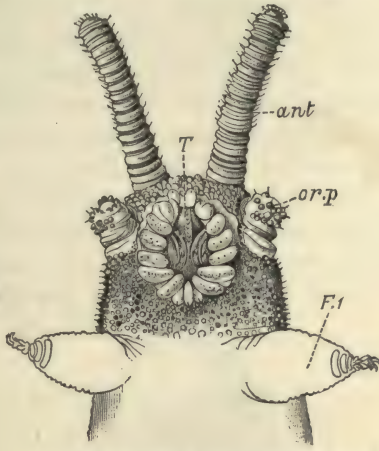


FIG. 333.—Ventral view of the head of *P. capensis* (after Sedgwick): *ant* antennae; *or.p* oral papillae; *F.1* first leg; *T* tongue.

the skin pigment is darker than elsewhere. The skin has a velvety texture and the colouring, which is always remarkable, varies considerably in the different species, and even in different individuals of the same species. The ventral surface is nearly always flesh-coloured, while the dorsal surface has a darker colour. In the South African species the colour of the dorsal surface varies from a dark green graduating to a bluish gray, to a brown varying to a red orange. The colour of the Australasian species varies in like manner, while that of the Neotropical, Malayan and New Britain species is less variable. The brown ground pigments are dissolved by spirit, but the other pigments are not appreciably affected.

The skin is thrown into a number of transverse ridges, along which wart-like papillae are placed. The papillae, which are found everywhere, are specially developed on the dorsal surface, less so on the ventral. Each papilla carries at its extremity a well-marked spine. The cuticle which covers the body is

everywhere, except on the lips and one or two other places, raised into minute *secondary papillae* or *scales* (Fig. 340) which may be pointed or blunt; each of them is in relation with a subjacent epidermal cell in which the skin pigment is contained.

The appendages of the head are the antennae, the jaws and the oral papillae.

The antennae, which are prolongations of the dorso-lateral parts of the head, are ringed, and taper slightly till near their termination, where they are slightly enlarged. The rings bear a number of spines, and the free end of the antennae is covered by a cap of spiniferous tissue like that of the rings.

The mouth is at the hinder end of a depression called the buccal cavity, and is surrounded by an annular tumid lip, raised into papilliform ridges and bearing a few spines (Fig. 333). Within the buccal cavity are the two jaws. They are short,

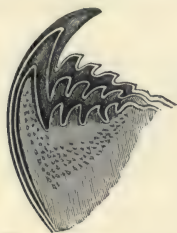


FIG. 334.—Inner jaw-claw of *P. capensis* (after Balfour).

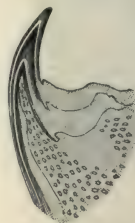


FIG. 335.—Outer jaw-claw of *P. capensis* (after Balfour).

stump-like, muscular structures, armed at their free extremities by a pair of cutting blades or claws, and are placed one on each side of the mouth. In the median line of the buccal cavity in front is placed a thick muscular protuberance, which may be called the tongue, though attached to the dorsal instead of to the ventral wall of the mouth (Fig. 333). The tongue bears a row of small chitinous teeth. The jaw-claws (Figs. 334 and 335), which resemble in all essential points the claws borne by the feet, and like these are thickenings of the cuticle, are sickle-shaped. They have their convex edge directed forwards and their concave or cutting edge turned backwards. The inner cutting plate (Fig. 334) usually bears a number of cutting teeth in addition to the main tooth. In some species the majority of these are separated by a diastema from the others and

arranged as a saw-like row of denticles. The jaws appear to be used for tearing the food, to which the mouth adheres by means of the tumid suctorial lips. The oral papillae are placed at the sides of the head (Fig. 333, *or.p*). The ducts of the slime-glands open at their free end. They possess two main rings of projecting tissue, and their extremities bear papillae irregularly arranged.

The ambulatory appendages vary in number. There are seventeen pairs in *P. capensis* and eighteen in *P. Balfouri*, while in *P. jamaicensis* the number varies from twenty-nine to forty-three pairs. They consist of two main divisions, which we may

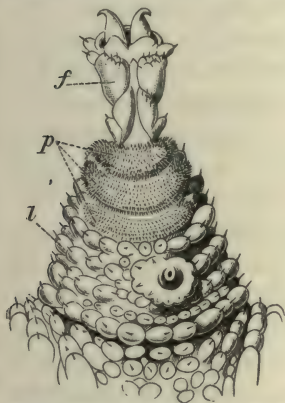


FIG. 336.—Ventral view of last leg of a male *P. capensis* (after Sedgwick). *f* Foot; *l* leg; *p* spiniferous pads. The white papilla on the proximal part of this leg is characteristic of the male of this species.

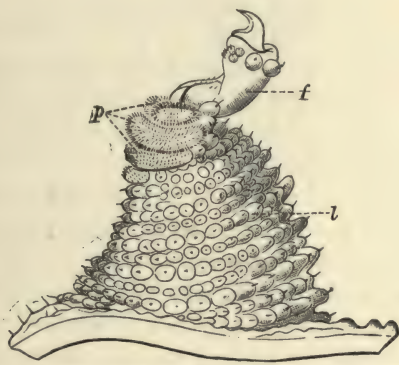


FIG. 337.—Leg of *P. capensis* seen from the front (after Sedgwick). *f* foot; *l* leg; *p* spiniferous pads.

call the leg and the foot (Figs. 336 and 337). The leg (*l*) has the form of a truncated cone, the broad end of which is attached to the ventro-lateral wall of the body, of which it is a prolongation. It is marked by a number of rings of papillae placed transversely to its long axis, the dorsal of which are pigmented like the dorsal surface of the body, and the ventral like the ventral surface. At the narrow distal end of the leg there are, on the ventral surface, three or four (rarely five, six, or seven) spiniferous pads, each of which is continued dorsally into a row of papillae. The foot (*f*) is attached to the distal end of the leg. It is slightly narrower at its attached extremity than at its free end. It bears two sickle-shaped claws and two, three or

four (rarely more) papillae. The part of the foot which carries the claws is especially retractile, and is generally found more or less telescoped into the proximal part. The legs of the fourth and fifth pairs differ from the others in the fact that the enlarged nephridia of these segments open upon, or in close relation with the proximal spiniferous pad.

In some species certain of the legs bear on their ventral sides furrows with tumid lips and lined by smooth non-tuberculate epithelium; they are called **coxal organs**. In some forms (S. African, etc.) they are very faintly indicated; in others (neotropical, etc.) they are considerably deepened to form the so-called coxal vesicles, which, it is stated, can be everted.

The males are generally rather smaller and less numerous than the females. In those species in which the number of legs varies, the male has a smaller number of legs than the female.

The **slime glands** open at the end of the oral papillae and are contained in the central compartment of the body-cavity in which they form conspicuous objects. Their ducts are considerably dilated to form the large slime-reservoirs (Fig. 338 *sl.d.*), and the gland itself is tubular (*sl.g.*), the tubes branching off from the posterior end of the duct. The slime is a viscid, albuminous fluid which hardens into threads in the air. Though non-acrid and harmless, it adheres to all objects which it touches except the skin of the animal itself. Its ejection is caused by the contraction of the muscular body-wall of the animal and it can be shot out to a considerable distance. It is used to entangle the more active prey, but it has to be used sparingly, for after a few ejections the supply stored in the reservoirs is exhausted.

The **Alimentary Canal** (Fig. 338). The buccal cavity, as explained above, is a secondary formation around the true mouth, which is at its dorsal posterior end. It contains the tongue and the jaws, which have already been described, and into the hind end of it there open ventrally by a median opening the salivary glands (*s.g.*). The mouth leads into a muscular pharynx (*ph.*), which is connected by a short oesophagus (*oe.*) with a stomach (*st.*). The stomach forms by far the largest part of the alimentary canal. It is a dilated soft-walled tube, and leads behind into the short rectum (*R.*), which is slightly curved and opens at the anus. There are no glands opening into the alimentary canal.

The **salivary glands**, which open into the buccal cavity, are

placed in the lateral compartments of the body-cavity immediately dorsal to the ventral nerve cords and extend backwards for a very variable distance in the different species (Fig. 338, *s.g.*), sometimes for not more than half the length of the body and sometimes for nearly its whole length. Immediately behind the mouth and in front of the first pair of legs they bend inwards and ventralwards and fall, one on each side, into the narrow hind end of the buccal cavity. They consist of an unbranched tube on each side, the lining of which is the glandular tissue of the gland and the front end of which receives the opening of a vesicle with vacuolated protoplasmic wall. The salivary glands are the nephridia of the segment of the oral papillae and the just-mentioned vesicles are their end-sacs.

The **central nervous system** consists of a pair of supra-oesophageal ganglia united in the middle line, and of a pair of widely divaricated ventral cords, continuous in front with the supra-oesophageal ganglia (Fig. 339).

The ventral cords at first sight appear to be without ganglionic thickenings, but on more careful examination they are found to be enlarged at the level of each pair of legs (Fig. 339). These enlargements may be regarded as imperfect ganglia. There are, therefore, as many

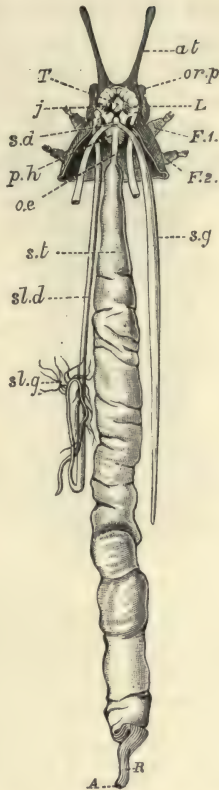


FIG. 338.—*Peripatus capensis* dissected so as to show the alimentary canal, slime glands, and salivary glands (after Balfour). The dissection is viewed from the ventral side, and the lips (*L*) have been cut through in the middle line behind and pulled outwards so as to expose the jaws (*j*), which have been turned outwards, and the tongue (*T*) bearing a median row of chitinous teeth, which branches behind into two. The muscular pharynx, extending back into the space between the first and second pairs of legs, is followed by a short tubular oesophagus. The latter opens into the large stomach with plicated walls, extending almost to the hind end of the animal. The stomach at its point of junction with the rectum presents an S-shaped ventro-dorsal curve. *A* anus; *at* antenna; *F.1*, *F.2* first and second legs; *j* jaws; *L* lips; *oe* oesophagus; *or.p* oral papilla; *ph* pharynx; *R* rectum; *s.d* salivary duct; *s.g* salivary gland; *sl.d* slime duct; *sl.g* salivary reservoir; *st* stomach; *T*, tongue in roof of mouth.

ganglia as there are legs. There is in addition a ganglionic enlargement at the commencement of the oesophageal commissures, where the nerves to the oral papillae are given off (Fig. 339, *orn*).

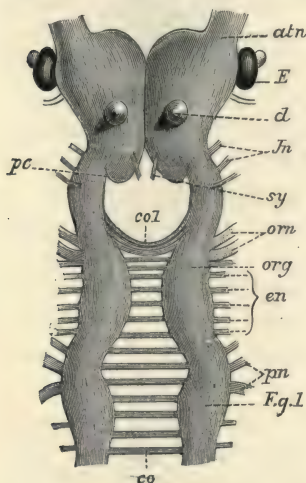


FIG. 339.—Brain and anterior part of the ventral nerve-cords of *Peripatus capensis* enlarged and viewed from the ventral surface (after Balfour). The paired appendages (*d*) of the ventral surface of the brain are seen, and the pair of sympathetic nerves (*sy*) arising from the ventral surface of the hinder part. From the commencement of the oesophageal commissures pass off on each side a pair of nerves to the jaws (*Jn*). The three anterior commissures between the ventral nerve-cords are placed close together; immediately behind them the nerve-cords are swollen, to form the ganglionic enlargements from which pass off to the oral papillae a pair of large nerves on each side (*orn*). Behind this the cords present a series of enlargements, one pair for each pair of legs, from which a pair of large nerves pass off on each side to the legs (*pn*). *atn* Antennary nerves; *co* commissures between ventral cords; *d* ventral appendages of brain; *E* eye; *en* nerves passing outwards from ventral cord; *F.g.l* ganglionic enlargements from which nerves to legs pass off; *jn* nerves to jaws; *org* ganglionic enlargement from which nerves to oral papillae pass off; *orn* nerves to oral papillae; *pc* posterior lobe of brain; *pn* nerves to legs; *sy* sympathetic nerves.

The ventral cords are placed each in the lateral compartments of the body cavity, immediately within the longitudinal layer of muscles. They are connected with each other, rather like the pedal nerves of *Chiton* and the lower Prosobranchiata, by a number of commissures. These commissures exhibit a fairly regular arrangement from the region included between the first and the last pair of true legs. There are nine or ten of them between each pair of legs. They pass along the ventral wall of the body, perforating the ventral mass of longitudinal muscles. On their way they give off nerves which innervate the skin. Posteriorly the two nerve-cords nearly meet immediately in front of the generative aperture, and then, bending upwards, fall into each other dorsal to the rectum. They give off a series of nerves from their outer borders, which present throughout the trunk a fairly regular arrangement. From each ganglion two large nerves (*pn*) are given off, which, diverging somewhat from each other, pass into the legs.

From the oesophageal commissures, close to their junction with the supra-oesophageal ganglia, a nerve arises on each side which passes to the jaws, and a little in front of this, apparently

from the supra-oesophageal ganglion itself, a second nerve to the jaws also takes its origin.

The supra-oesophageal ganglia (Fig. 339) are large, somewhat oval masses, broader in front than behind, completely fused in the middle, but free at their extremities. Each of them is prolonged anteriorly into an antennary nerve, and is continuous behind with one of the oesophageal commissures. On the ventral surface of each, rather behind the level of the eye, is placed a hollow protuberance (Fig. 339, *d*), of which we shall say more in dealing with the development. About one-third of the way back the two large optic nerves take their origin, arising laterally, but rather from the dorsal surface (Fig. 339). Each of them joins a large ganglionic mass placed immediately behind the retina.

The histology of the ventral cords and oesophageal commissures is very simple and uniform. They consist of a cord formed of nerve-fibres placed dorsally, and of a ventral layer of ganglion cells.

The eyes (Fig. 340) consist of hollow vesicles, the cavity of which is occupied by a cuticular lens (*l*). The front wall consists of a layer of somewhat cubical epithelial cells lying immediately beneath the cornea (*cor*), and the hinder wall is much thickened, consisting of retina (*Re*) and of pigment (*pi.r*). The optic ganglion is closely applied against the pigment. The cuticle over the eye is thin and transparent and lies immediately over the epidermis which here constitutes the corneal epithelium. The eye is developed as an invagination of the embryonic brain while it is still part of the ectoderm, and its connexion with the brain by means of the optic nerve is a persistent remains of this primitive connexion.

The skin is formed of three layers. (1) The cuticle. (2) The epidermis or hypodermis. (3) The dermis.

The cuticle is a thin layer. The spines, jaws, and claws are special developments of it. Its surface is not, however, smooth, but is everywhere, with the exception of the perioral region, raised into minute secondary papillae, which in most instances bear at their free extremity a somewhat prominent spine. The whole surface of each of the secondary papillae just described is in its turn covered by numerous minute spinous tubercles.

The epidermis, placed immediately within the cuticle, is

composed of a single layer of cells, which vary, however, a good deal in size in different regions of the body. The cells excrete the cuticle, and they stand in a very remarkable relation to the secondary papillae of the cuticle just described. Each epidermis cell is in fact placed within one of these secondary papillae, so that the cuticle of each secondary papilla is the product of a single epidermis cell. The pigment which gives the characteristic colour to the skin is deposited in the protoplasm of the outer ends of the cells in the form of small granules.

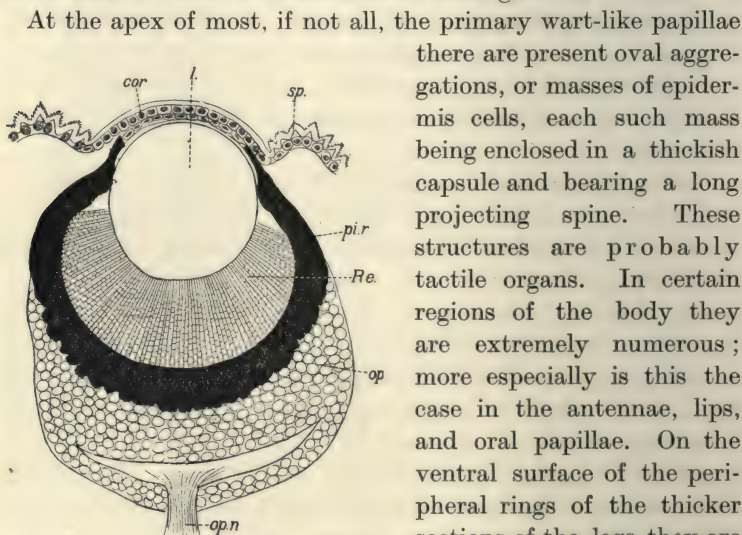


FIG. 340.—Eye of *Peripatus capensis* as shown in a longitudinal section through the head (partly diagrammatic). *cor* Cornea; *l* lens; *op* optic ganglion; *op.n* optic nerve; *pi.r* pigment; *Re* retina; *sp* secondary papillae of skin (after Balfour).

there are present oval aggregations, or masses of epidermis cells, each such mass being enclosed in a thickish capsule and bearing a long projecting spine. These structures are probably tactile organs. In certain regions of the body they are extremely numerous; more especially is this the case in the antennae, lips, and oral papillae. On the ventral surface of the peripheral rings of the thicker sections of the legs they are also very thickly set and fused together so as to form a kind of pad (Figs. 336 and 337). In the antennae

they are thickly set side by side on the rings of skin which give such an arthropodan appearance to these organs in *Peripatus*.

The apertures of the **tracheal system** are placed in the depressions between the papillae or ridges of the skin. Each of them leads into a tube, which may be called the tracheal pit (Fig. 341), the walls of which are formed of epithelial cells bounded towards the lumen of the pit by a very delicate cuticular membrane continuous with the cuticle covering the surface of the body. The pits vary somewhat in depth; the pit figured was about 0.09 mm.

It perforates the dermis and terminates in the subjacent muscular layer.

Internally it expands in the transverse plane and from the expanded portion the tracheal tubes arise in diverging bundles. Nuclei similar in character to those in the walls of the tracheal pit are placed between the tracheae, and similar but slightly more elongated nuclei are found along the bundles. The tracheae are minute tubes exhibiting a faint transverse striation which is probably the indication of a spiral fibre. They appear to branch, but only exceptionally. The tracheal apertures are diffused over the surface of the body, but are especially developed in certain regions.

The general **muscular system** consists of—(1) the general wall of the body; (2) the muscles connected with the mouth, pharynx and jaws; (3) the muscles of the feet; (4) the muscles of the alimentary

tract. The muscular wall of the body is formed of—(1) an external layer of circular fibres; (2) an internal layer of longitudinal muscles. The main muscles of the body are unstriated and divided into fibres, each invested by a delicate membrane. The muscles of the jaws alone are transversely striated.

The **vascular system** consists of a dorsal tubular heart with paired ostia leading into it from the pericardium, of the pericardium, and the various other divisions of the perivisceral cavity (Fig. 345 D). As in all Arthropoda, the perivisceral cavity is a haemocoel; i.e. it contains blood and forms part of the vascular system. The heart extends from close to the hind end of the body to the head. There do not appear to be any definite blood-vessels, other than the heart.

The **body cavity** is formed of four compartments—one central,

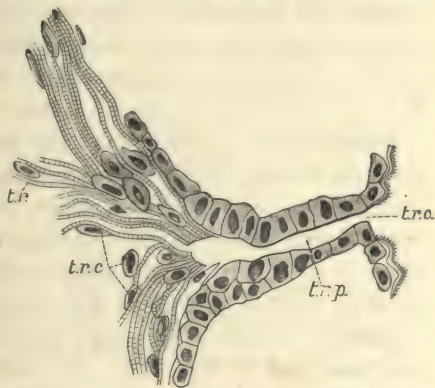


FIG. 341.—Section through a tracheal pit and diverging bundles of tracheal tubes taken transversely to the long axis of the body (after Balfour). *tr.* Tracheae showing rudimentary spiral fibre; *tr.c.* cells resembling those lining the tracheal pits, which occur at intervals along the course of the tracheae; *tr.o.* tracheal stigma; *tr.p.* tracheal pit.

two lateral, and a pericardial (Fig. 345 *D*). The former is by far the largest, and contains the alimentary tract, the generative organs, and the slime glands. It is lined by a delicate endothelial layer, and is not divided into compartments nor traversed by muscular fibres. The lateral divisions are much smaller than the central, and are shut off from it by the inner transverse band of muscles. They are almost entirely filled with the nerve-cord and salivary gland in front and with the nerve-cord alone behind, and their lumen is broken up by muscular bands. They further contain the nephridia. They are prolonged into the feet, as is the embryonic body cavity of most Arthropoda. The pericardium contains a peculiar cellular tissue, probably, as suggested by Moseley, equivalent to the fat-bodies of insects.

Nephridia are present in all the legs, excepting those of the segment bearing the genital opening. Most of them are constructed in a very similar manner, while the two pairs situated in the fourth and fifth pairs of legs are considerably larger than those behind, and are in some respects very differently constituted, and the first three pairs show some reduction.

A nephridium from the ninth pair of legs of *Peripatus capensis* is represented in Fig. 342. The external opening is placed at the inner end of a transverse groove (coxal organ) at the base of one of the legs, while the main portion of the organ lies in the body cavity in the base of the leg, and extends into the trunk to about the level of the outer edge of the nerve-cord of its side. The external opening (*o.s*) leads into a narrow tube (*s.d*), which gradually dilates into a large sac (*s*). The narrow part is lined by small epithelial cells, which are directly continuous with and perfectly similar to those of the epidermis. The sac itself, which forms a kind of bladder or collecting vesicle for the organ, is provided with an extremely thin wall, lined with very large flattened cells. The second section of the nephridium is formed by the coiled tube, the epithelial lining of which varies slightly in the different parts. The third section (*s.o.t*), constitutes the most distinct portion of the whole organ. Its walls are formed of columnar cells almost filled by oval nuclei, which absorb colouring matters with very great avidity, and thus render this part extremely conspicuous. The nuclei are arranged in several rows. It ends by opening into a vesicle (Fig. 345 *D*), the wall of which is so delicate that it is destroyed when the nephridium

is removed from the body, and consequently is not shown in Fig. 342. This internal vesicle was discovered by Sedgwick and is known as the end-sac. Its discovery was of considerable morphological importance not only because it cleared up the question of the arthropod body-cavity, but also because it threw considerable light upon the general theory of the coelom.

The fourth and fifth pairs are very considerably larger than those behind, and are in other respects peculiar. The great mass of each organ is placed behind the leg on which the external opening is placed, immediately outside one of the lateral nerve-cords. The external opening, instead of being placed near the base of the leg, is placed on the ventral side of or in close relation with the proximal spiniferous pad. It leads into a portion which clearly corresponds with the collecting vesicle of the hinder nephridia. This part is not, however, dilated into a vesicle. The three pairs of nephridia in the three foremost pairs of legs are rudimentary, consisting solely of a vesicle and duct. The salivary glands are the modified nephridia of the segment of the oral papillae.

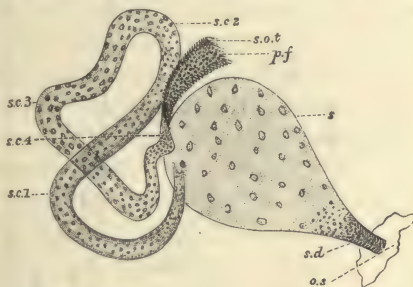


FIG. 342.—Nephridium from the 9th pair of legs of *P. capensis*. *o.s.* External opening of segmental organ; *p.f.* Internal opening of nephridium into the body cavity (lateral compartment); *s* vesicle of segmental organ; *s.c.1*, *s.c.2*, *s.c.3*, *s.c.4* successive regions of coiled portion of nephridium; *s.o.t.* third portion of nephridium broken off at *p.f.* from the internal vesicle, which is not shown (after Balfour).

The **crural glands** are seen at their simplest in *P. capensis*, in which they are present in both sexes and in all the legs except the first. They open externally to the nephridia (except in legs 4 and 5) and consist of a glandular vesicular body contained in the pedal compartment of the body cavity and communicating with the exterior by a narrow duct. They are absent in *P. novae-zealandiae* and *novae-britanniae*. As a rule they are only present in the male. There may be two pairs of them in each leg and their opening is often placed on a prominent papilla (many legs of the neotropical species, last leg in male of Cape species, Fig. 336).

Generative Organs. The male organs (Fig. 343) consist of a pair of testes (*te*), a pair of vesicles (*v*), vasa deferentia (*v.d*), and accessory glandular tubules (*f*). All the above parts lie in the central compartment of the body cavity. In *P. capensis* the crural glands of the last (17th) pair of legs are enlarged and prolonged into an elongated tube (*a.g*) placed in the lateral compartment of the body cavity. The right vas deferens passes, in *P. capensis*, under both nerve-cords to join the left, and form the enlarged tube (*p*), which, passing beneath the nerve-cord of its side, runs to the external orifice. The enlarged

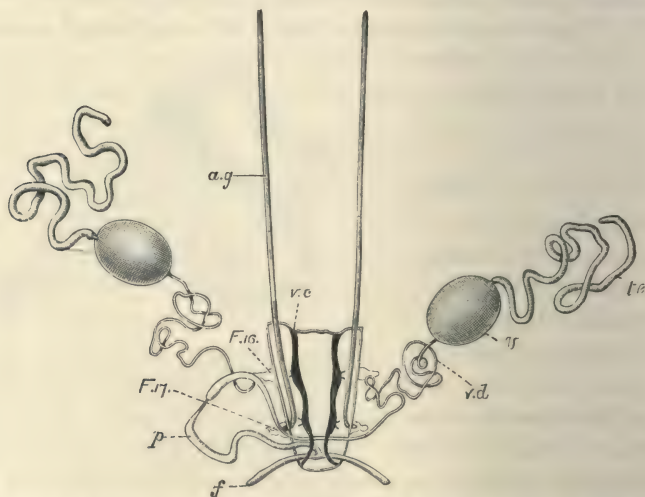


FIG. 343.—Male generative organs of *Peripatus capensis*, viewed from the dorsal surface (after Balfour). *a.g* Enlarged crural glands of last pair of legs; *F.16, 17*, last pairs of legs; *f* small accessory glandular tubes; *p* common duct into which the vasa deferentia open; *te* testis; *v* seminal vesicle; *v.c* nerve-cord; *v.d* vas deferens.

terminal portion possesses thick muscular walls, which serve for the extrusion of the spermatophores. In some specimens a different arrangement obtains, in that the left vas deferens passes under both nerve-cords to join the right. The length of the unpaired part of the vas deferens varies considerably in length in the different groups of species. In the Cape species it is of no great length, and the accessory glands open into its terminal portion. In other species these glands open directly to the exterior and independently of the vas deferens. The spermatozoa* are long and thread-like. The head tapers at

* T. H. Montgomery, *Zool. Jahrb.* 14, 1900, p. 277.

its free end, and its other end is prolonged, without any diminution in thickness, as the tail.

FEMALE.—The ovaries (Fig. 343 *bis*) consist of a pair of tubes closely applied together, and continued posteriorly into the oviducts. The oviducts, after a short course, become dilated into the uteruses, which join behind and open to the exterior by the median genital opening. The two ovaries are bound together in a common muscular sheath and are connected to the floor of the pericardium in the posterior part of the body cavity either by a cord (the *funiculus*, 1) proceeding from their morphological front end (end remote from entrance of oviduct), or along their whole length by a kind of mesentery. In *P. Tholloni* and a few neotropical species the ovaries are unattached and float freely in the body-cavity. The ova are produced by the epithelium of the ovarian tubes (*endogenous*, as in the neotropical species, Fig. 343 *bis*) or are developed in follicular outgrowths of the ovaries (*exogenous*, as in the Cape, Australasian and New Britain forms). Occasionally the ovarian tubes communicate; this is carried furthest in the Malayan species in which they are completely united to form one ovarian sac. In *P. Tholloni* the opposite extreme is found, the ovaries as well as the oviducts being entirely separate from one another. Except in the last named species the oviducts are always united at their point of junction with the ovary.

The ovaries often contain spermatozoa, some of which project through the ovarian wall into the body-cavity, so that the ovary has almost a hairy appearance in freshly dissected specimens. Spermatozoa are not found in the uterus and oviducts and it is not known how they reach the ovaries or receptacula seminis (see below). In most of the species there is a globular receptaculum seminis (4) opening by two short ducts close together into the oviduct, and in the neotropical and Malayan species and in *P. Tholloni* there is a small receptaculum ovorum with extremely thin walls opening into the oviduct by a short duct just in front of the receptaculum seminis (Fig. 343 *bis*, 3). The epithelium of the latter structure is clothed with actively moving cilia, at least in the neotropical species. The receptacula seminis usually contain spermatozoa which are then absent from or sparse in the ovaries. In *Neo-Peripatus* eggs are present in the receptacula ovorum.

External sexual differences (p. 576) are sometimes afforded by the shape of the genital opening and sometimes by the openings of the accessory glands of the male. In many species the apertures of the crural glands, or of some of them, are placed on enlarged white papillae. This occurs on the last leg of the male

in the Cape species (Fig. 336), in some of the Australasian and in most neotropical species.

Habits.* In their natural haunts they form exceedingly beautiful and surprising objects. They live beneath the bark of rotten stumps of trees, in the crevices of rock, and beneath stones. They require a moist atmosphere, and are exceedingly susceptible to drought. They avoid light, and are therefore rarely seen. They move with great deliberation, picking their course by means of their antennae and eyes. It is by the former that they acquire a knowledge of the ground over which they are travelling, and by the latter that they avoid the light. The antennae are extraordinarily sensitive, and so delicate, indeed, that

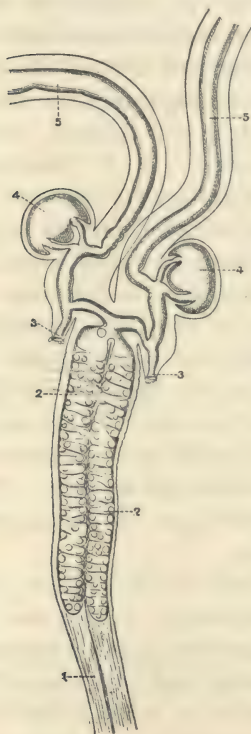


FIG. 343 bis.—Female generative organs of *Peripatus trinidadensis* (after Gaßron). 1 Funiculus; 2 ovary; 3 duct or funnel of receptaculum ovarum, the latter not being shown; 4 receptaculum seminis; 5 anterior end of uterus.

they seem to be able to perceive the nature of objects without actual contact. When irritated they eject with considerable force the contents of their slime reservoirs from the oral papillae. The force is supplied by the sudden contraction of the muscular body wall. They can squirt the slime to the distance of almost

* Thos. Steel, *Proc. Lin. Soc. New S. Wales*, 1896, p. 94.

a foot. The slime, which appears to be perfectly harmless, is extremely sticky, but it easily comes away from the skin of the animal itself. Hutton describes the New Zealand species as using this apparatus for the capture of prey. It appears also to be used as a defensive weapon. They will turn their heads to any part of the body which is being irritated and violently discharge their slime at the offending object. Locomotion is effected entirely by means of the legs, with the body fully extended.

Of their food in the natural state we know little; but it is probably mainly, if not entirely, animal. Hutton describes his specimens as sucking the juices of flies which they had stuck down with their slime, and Steel describes their consumption of woodlice, termites, etc. Those kept in captivity eagerly devour the entrails of their fellows, and the developing young from the uterus. They also like raw sheep's liver. They move their mouths in a suctorial manner, tearing the food with their jaws. They have the power of extruding their jaws from the mouth, and of working them alternately backwards or forwards. This is readily observed in individuals immersed in water. They do not eat one another, nor do they attack their young even when kept without food. They are often found together and appear to live in perfect harmony. They are exceedingly local in their occurrence and are rarely found in numbers. They cast their skin at irregular intervals and the moulted cuticle is often eaten. When kept in captivity they will creep at night through the smallest aperture and so escape.

Breeding. Almost all species are viviparous, but one or two of the Australasian species are normally oviparous and lay eggs with a sculptured shell. All Australasian species come near to laying eggs, inasmuch as the eggs are large, full of yolk, and enclosed in a shell; but, excepting the species referred to, development takes place in the uterus, though, abnormally, incompletely developed eggs are extruded.

The young of *P. capensis* are born in April and May. They are almost colourless at birth, excepting the antennae, which are green, and their length is 10 to 15 mm. A large female will produce thirty to forty young in one year. The period of gestation is thirteen months, that is to say, the ova pass into the oviducts about one month before the young of the preceding year, all of which are practically of the same age, are born. They are

born one by one, and it takes some time for a female to get rid of her whole stock of embryos ; in fact, the embryos in any given female differ slightly in age, those next the oviduct being a little younger (a few hours) than those next the vagina. The mother does not appear to pay any special attention to her young, which wander away and get their own food. There does not appear to be any true copulation. The male deposits small, white, oval spermatophores, which consist of small bundles of spermatozoa cemented together by some glutinous substance, indiscriminately on any part of the body of the female and indeed of the male. Such spermatophores are found on the bodies of both males and females from July to January, but they appear to be most numerous in the autumn. It has been suggested that the spermatozoa make their way from the adherent spermatophore through the body wall into the body, and so by traversing the tissues reach the ovary ; but having regard to the thickness and the toughness of the skin and the absence of any cutaneous secretion capable of dissolving the coat of the spermatophore, it seems unlikely that this should occur. We therefore venture to make the suggestion, though we cannot offer any facts in support of it, except the swallowing of the cuticle above mentioned, that the creatures lick the spermatophores off their bodies or otherwise devour them and that the spermatozoa are set free in the stomach and make their way through its soft walls and through the body cavity to the ovary or receptaculum seminis. The testes are active from June to the following March. From March to June the vesiculae of the male are empty. In some species (Australasian, neotropical, etc.) the spermatophores are large and have horny cases ; nothing is known as to their deposition.

Whereas in the Cape species embryos in the same uterus are all practically of the same age (except in the month of April when two broods overlap in *P. capensis*), and birth takes place at a fixed season ; in other species the uterus, which is always pregnant, contains embryos of different ages, and births take place all the year round. In all species of *Peripatus* the young are fully formed at birth and differ from the adult in little more than in size and colour. The number of spiniferous rings on the antennae appears to increase by intercalation after birth and it is possible that there may be other slight additions, but speaking

generally the perfection of the animal at birth is a feature which pre-eminently distinguishes our genus and in which it is excelled by no other animal.

Development.—*Peripatus* is found in Africa, in Australasia, in South America and the West Indies, in New Britain, and in the Malay Peninsula and Sumatra. The species found in these various localities are closely similar in their anatomical characters, the principal differences relating to the structure of the female generative organs and to the number of the legs. They differ, however, in the most striking manner in the structure of the ovum and in the early development. In all the Australasian and Malayan species the egg is large and heavily charged with food-yolk, and is surrounded by a tough membrane. In the Cape species the eggs are smaller, though still of considerable size; the yolk is much less developed, and the egg membrane is thinner though dense. In the New Britain species the egg is still smaller (.1 mm.), and there is a large trophic vesicle. In the neotropical species the egg is minute, and almost entirely devoid of yolk. The unsegmented uterine ovum of *P. novae-zealandiae* measures 1.5 mm. in length by .8 mm. in breadth; that of *Eoperipatus Weldoni* about 1 mm. in its longest diameter; that of *P. capensis* is .56 mm. in length; and that of *P. trinidadensis* .04 mm. in diameter. In correspondence with these differences in the ovum there are differences in the early development, though the later stages are closely similar. The development has been worked out in *P. capensis*, to which species the following description refers. The ova are apparently fertilized in the ovary, and they pass into the oviducts in April and May. In May the brood of the preceding year are born, and the new ova, which have meanwhile undergone cleavage, pass into the uterus. There are ten to twenty ova in each uterus. The segmentation is peculiar, and leads to the formation of a solid gastrula, consisting of a cortex of ectodermal nuclei surrounding a central endodermal mass, which consists of a much-vacuolated tissue with some irregularly-shaped nuclei. The endoderm mass is exposed at one point—the blastopore (gastrula mouth). The central vacuoles of the endoderm now unite and form the enteron of the embryo, and at the same time the embryo elongates into a markedly oval form, and an opacity—the primitive streak—appears at the

hind end of the blastopore (Fig. 344 *B*). This elongation of the embryo is accompanied by an elongation of the blastopore, which soon becomes dumb-bell shaped (Fig. 344 *C*). At the same time the mesoblastic somites (embryonic segments of mesoderm) have made their appearance in pairs at the hind end, and gradually travel forward on each side of the blastopore to the front end, where the somites of the anterior pair soon meet in front of the blastopore (Fig. 344 *D*). Meanwhile the narrow middle part of the blastopore has closed by a fusion

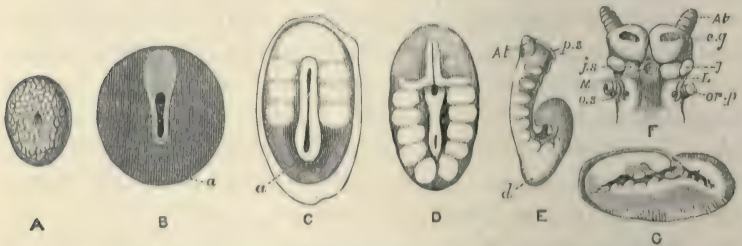


FIG. 344.—A series of embryos of *P. capensis*. The hind end of embryos *B*, *C*, *D* is uppermost in the figures, the primitive streak is the white patch behind the blastopore (after Sedgwick). *A* gastrula stage, ventral view, showing blastopore. *B* older gastrula stage, ventral view, showing elongated blastopore and primitive streak. *C* ventral view of embryo with three pairs of mesoblastic somites, dumb-bell-shaped blastopore and primitive streak. *D* ventral view of embryo, in which the blastopore has completely closed in its middle portion, and given rise to two openings, the embryonic mouth and anus. The anterior pair of somites have moved to the front end of the body, and the primitive groove has appeared on the primitive streak. *E* side view of embryo, in which the hind end of the body has begun to elongate in a spiral manner, and in which the appendages have begun. *At* antenna; *d* dorsal projection; *p.s* preoral somite. *F* ventral view of head of embryo intermediate between *E* and *G*. The cerebral grooves are wide and shallow. The lips have appeared, and have extended behind the openings of the salivary glands, but have not yet joined in the middle line. *At* antennae; *c.g* cerebral groove; *j* jaws; *j.s* swelling at base of jaws; *L* lips; *M* mouth; *or.p* oral papillae; *o.s* opening of salivary gland. *G* side view of older embryo with the full number of appendages, to show the position in which the embryos lie in the uterus.

of its lips, so that the blastopore is represented by two openings, the future mouth and anus. A primitive groove makes its appearance behind the blastopore (Fig. 344 *D*). At this stage the hind end of the body becomes curved ventrally into a spiral (Fig. 344 *E*), and at the same time the appendages appear as hollow processes of the body wall, a mesoblastic somite being prolonged into each of them. The first to appear are the antennae, into which the praeoral somites are prolonged. The remainder appear from before backwards in regular order, viz. jaws, oral papillae, legs 1–17. The full number of somites and their appendages is not, however, completed until a later stage. The nervous system is formed as an annular thickening of ecto-

derm passing in front of the mouth and behind the anus, and lying on each side of the blastopore along the lines of the somites. The praeoral part of this thickening, which gives rise to the cerebral ganglia, becomes pitted inwards on each side (Fig. 344 *F*, *c.g.*). These pits are eventually closed, and form the hollow ventral appendages of the supra-pharyngeal ganglia of the adult (Fig. 339, *d*). The lips are formed as folds of the side wall of the body, extending from the praeoral lobes to just behind the jaw (Fig. 344 *F*, *L*). They enclose the jaws (*j*), mouth (*M*), and opening of the salivary glands (*o.s.*), and so give rise to the buccal cavity. The embryo has now lost its spiral curvature, and becomes completely doubled upon itself, the hind end being in contact with the head (Fig. 344 *G*). It remains in this position until birth. The just-born young are from 10–15 mm. in length and have green antennae, but the rest of the body is either quite white or of a reddish colour. This red colouring matter differs from that of the adult in being more soluble in spirit.

The mesoderm is entirely formed from the proliferated ectoderm of the primitive streak, which closely resembles that of the vertebrata.

The mesoblastic somites are paired sacs formed from the anterior lateral portions of the primitive streak (Fig. 344 *C*). As they are formed they become placed in pairs on each side of the blastopore. The somites of the first pair eventually obtain a position entirely in front of the blastopore (Fig. 344 *D*). They form the somites of the praeoral lobes. The full complement of somites is acquired at about the stage of Fig. 344 *E*. The relations of the somites are shown in Fig. 345 *A*, which represents a transverse section taken between the mouth and anus of an embryo of the stage of Fig. 344 *D*. The history of these somites is an exceedingly interesting one, and may be described shortly as follows: They divide into two parts—a ventral part, which extends into the appendage, and a dorsal part (Fig. 345 *B*). The ventral part acquires an opening to the exterior just outside the nerve-cord, and becomes entirely transformed into a nephridium (Fig. 345 *D*, 2'). The dorsal part shifts dorsalwards and diminishes relatively in size (Fig. 345 *C*). Its fate differs in the different parts of the body. In the anterior somites it dwindles and disappears, but in the posterior part it unites with the dorsal divisions of contiguous somites of the same

side, and forms a tube—the generative tube (Fig. 345 *D*, 2). The last section of this tube retains its connexion with the ventral portion of the somite, and so acquires an external opening, which is at first lateral, but soon shifts to the middle line and fuses with its fellow, to form the single generative opening. The praeoral somite develops the rudiment of a nephridium, but eventually entirely disappears. The jaw somite also disappears

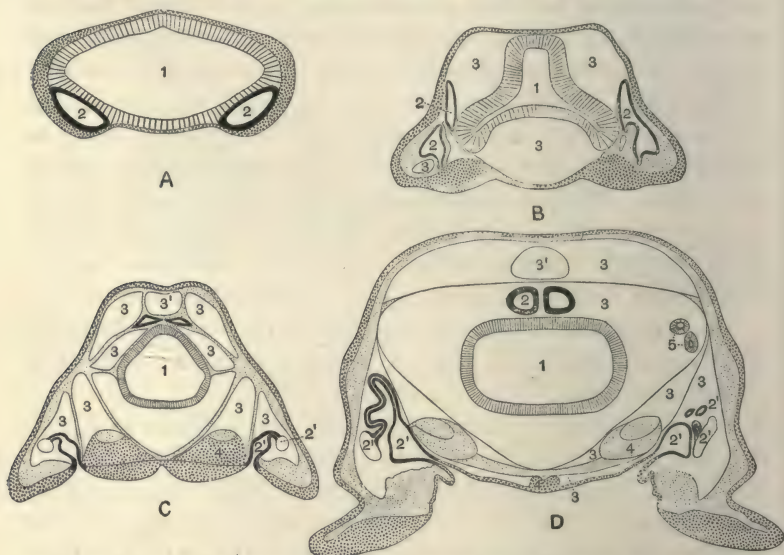


FIG. 345.—A series of diagrams of transverse sections through *Peripatus* embryos to show the relations of the coelom at successive stages (after Sedgwick). *A*, early stage: 1 gut; 2 mesoblastic somite; no trace of the vascular space; endoderm and ectoderm in contact. *B*, endoderm has separated from the dorsal and ventral ectoderm. The somite is represented as having divided on the left side into a dorsal and ventral portion: 1 gut; 2 somite; 3 haemocoel. *C*, The haemocoel (3) has become divided up into a number of spaces, the arrangement of which is unimportant. The dorsal part of each somite has travelled dorsalwards, and now constitutes a small space (triangular in section) just dorsal to the gut. The ventral portion (2') has assumed a tubular character, and has acquired an external opening. The internal vesicle is already indicated, and is shown in the diagram by the thinner black line: 1 gut; 2' nephridial part of coelom; 3 haemocoel; 3' part of haemocoel which will form the heart—the part of the haemocoel on each side of this will form the pericardium; 4 nerve-cord. *D* represents the conditions at the time of birth; numbers as in *C*, except 5, slime glands. The coelom is represented as surrounded by a thick black line, except in the part which forms the internal vesicle of the nephridium.

the somites of the oral papillae form ventrally the salivary glands, which are thus serially homologous with nephridia. The perivisceral cavity of *Peripatus* is, as in all Arthropoda, a haemocoel. Its various divisions develop as a series of spaces between the ectoderm and endoderm, and later in the mesoderm. The mesoderm seems to be formed entirely from the proliferation of the cells of the mesoblastic somites. It thus appears that in

Peripatus the coelom does not develop a perivisceral portion, but gives rise only to the renal and reproductive organs.

Peripatus Guilding. Soft-bodied vermiform animals, with one pair of ringed antennae, one pair of jaws, one pair of oral papillae, and a varying number of claw-bearing ambulatory legs. Dorsal surface arched and more darkly pigmented than the flat ventral surface. Skin transversely ridged and beset by wart-like spiniferous papillae. Mouth anterior, ventral; anus posterior, terminal. Generative opening single, median, ventral, and posterior. One pair of simple eyes. Brain large with two ventral hollow appendages; ventral cords widely divaricated, without distinct ganglia. Alimentary canal simple, uncoiled. Segmentally arranged, paired nephridia are present. Body cavity is continuous with the vascular system, and does not communicate with the paired nephridia. Heart tubular, with paired ostia. Respiration by means of tracheae. Dioecious; males smaller and generally less numerous than females. Generative glands tubular, continuous with the ducts. Viviparous (except two or three of the Australasian species), the young being born fully developed. They shun the light, and live in damp places beneath stones, leaves, and bark of rotten stumps. They eject when irritated a viscid fluid through openings at the apex of the oral papillae.

Distribution: South Africa, Australasia (Australia, N. Zealand, Tasmania), New Britain, South America and West Indies, Malaya (Malay Peninsula and Sumatra), Equatorial Africa, and Chili.

The species, of which between 50 and 60 are known, fall into seven discontinuous geographical groups, the members of which are more closely related to each other than to those of any other group. Although we deprecate as unnecessary the elevation of these groups in the present state of knowledge to the rank of genera, we think that it would be convenient to give them names which would connect them with their respective geographical areas. The names and distribution of these groups, together with the generic names which have been applied to them by various authors are as follows:—

Neo-Peripatus (*Peripatus*). Neotropical Region (West Indies and America from Mexico in the North to Rio de Janeiro in the South). 29 species.

Congo-Peripatus (*Mesoperipatus* Evans). Congo district in West Africa. 1 species.

Eo-Peripatus (*Eoperipatus* Evans). Malaya (Malacca and Sumatra). 4 species.

Capo-Peripatus (including *Peripatopsis* Pocock and *Opisthopatus* Purcell). South Africa (Natal to Cape Town). 7 species.

Melano-Peripatus (*Paraperipatus* Willey). Melanesia (New Britain). 1 species.

Austro-Peripatus (*Peripatoides* Pocock and *Ooperipatus* Dendy). Australasia (Australia, Tasmania, New Zealand). 8 species.

Chilio-Peripatus (*Opisthoptaus* Bouvier). Chili. 1 species.

N.B.—The characters marked with an * are peculiar to the group in which it is found.

Neo-Peripatus is generally distributed in the neotropical Region from Rio de Janeiro to Mexico and in the West Indian Islands. West of the Andes its southern limit appears to be Bolivia. The species on the high

plateaux and western slopes of the Andes (Andean) differ in certain points from the others (Caribbean). Its characters are : (1) The number of legs (23-43 pairs) is variable in the same species. (2) The inner jaw-blade has a diastema and a saw of denticles. (3) Legs with 4-7 spinous pads. (4) Nephridial openings of legs 4 and 5 on the proximal side of the 4th pad, either attached to it or separate from it. (5) Feet with 3 (Caribbean) or from 4-7 (Andean) distal papillae. (6) The genital opening is between the legs of the penultimate pair. (7) The oviduct is provided with a receptaculum seminis which contains spermatozoa and has 2 ducts, and with a receptaculum ovorum. (8) The ovary is endogenous. (9) The ova are minute (.04 mm. in diameter). (10) Embryos in the same uterus of all ages. (11) Unpaired part of vas deferens long. (12) Spermatophores elongated and with a thick case. (13) Skin-pigment brownish and affected by alcohol. (14) Legs with well-developed coxal organs. (15) Crural glands on many legs in the males. (16) Accessory glands of the male open separately at the sides of the anus.

The species of this group are very constant in the characters mentioned except in those of the legs and feet. This is an interesting point considering the wide area over which they range and the diverse conditions to which they are subjected.

The principal species are : Andean, *ecuadorensis* Bouv., *Lankesteri* Bouv., *tuberculatus* Bouv., *quitensis* Schmarda, *Cameranoi* Bouv., *Eiseni* Wheeler, etc. ; Caribbean, *jamaicensis* Grab. and Cock., *Sedgwicki* Bouv., *juliformis* Guilding, *trinidadensis* Sedgw., *Edwardsii* Blanchard, etc.

Congo-Peripatus. A single species, *P. Tholloni*, has been described by Bouvier from the French Congo. It is quite distinct from the other African *Peripatus* and must be regarded as a distinct type. Its characters are : (1) Number of legs (24-27 pairs) variable in the same species. (2) Inner jaw with a diastema and a saw of denticles. (3) Legs with 3 spinous pads. (4) Nephridial openings of legs 4 and 5 on the proximal side of the 3rd pad and attached to it. (5) Feet with 3 distal papillae (2 in front and 1 behind). (6) Genital opening between the legs of the penultimate pair. (7) Oviduct with a receptaculum seminis with 2 ducts, and a receptacula ovorum. (8) Character of ovary not described. (9) Ova minute, but size not determined. (10) Uterine embryos differ much in age ; * those near the genital opening lie in a large uterine dilatation. (11) Unpaired part of vas deferens long. (12) ? (13) Skin-pigment brownish, affected by alcohol. (14) Legs with well-developed coxal organs. (15) Crural glands in the two pairs of legs preceding the genital legs in the male, open on papillae. (16) Accessory glands of the male open in front of the anus in a common furrow. In addition to these characters the oviducts and ovaries are completely separate from one another, a feature found in no other species. This combination of characters is unique and there is no reason why the species should be associated with *Neo-Peripatus* as has been done by Bouvier.

Eo-Peripatus. Malacca (3 species) and Sumatra (1 species). The characters are : (1) Number of legs (23-25 pairs) usually variable in the same species. (2) Inner jaw with a diastema and saw of denticles. (3) Legs with 4 spinous pads. (4) * Nephridial openings of legs 4 and 5 either in the proximal pad or proximal to it. (5) * Feet with two distal papillae. (6) Genital opening between the legs of the penultimate pair. (7) Receptacula seminis with 2 ducts, and receptacula ovorum are present. (8) Ovary exogenous. (9) Ova large and heavily yolked (about 1 mm.

in longest diameter). (10) Uterine embryos of all ages. (11) Unpaired part of vas deferens long. (12) Spermatophore elongated, without a horny coat, but with a horny cap at one end. (13) Skin pigment brownish, not stated to be affected by alcohol. (14) Legs with well-developed coxal organs. (15) Crural glands in the male in the two pairs of legs preceding the genital opening, without papillae. (16) Accessory glands of the male open between the legs of the last pair by a common opening. In addition, the ovaries are completely fused and contain one spacious cavity, a character found in no other group of species. This group of species is specially interesting in possessing a large yolked ovum, a most important character and found elsewhere only in Austro-Peripatus. It is more clearly marked off from other species than any of the groups. The species are *P. Weldoni*, *P. Horsti*, *P. Bulleri*, and *P. sumatranus*.

Melano-Peripatus. New Britain (1 species, *P. novae-britanniae*). The characters are : (1) Number of legs (22-24 pairs) is variable in the species. (2) The outer jaw is without a minor tooth, and the inner jaw has no diastema or saw. (3) Legs with 3 spinous pads. (4) Nephridial openings of legs 4 and 5 on the proximal pad. (5) Feet with 3 distal papillae, one of which is anterior, one dorsal, and one anterior. (6)* Genital opening subterminal, behind the legs of the last pair. (7) Oviduct with a receptaculum seminis with 2 ducts, without a receptaculum ovorum. (8) Ovary exogenous. (9)* Ova of medium size (.1 mm. in longest diameter) (with little yolk). (10) Embryos of all ages in the same uterus. (11) Unpaired part of vas deferens very short, almost obsolete. (12)* Spermatophores absent. (13) Skin-pigment black, apparently not affected by spirit. (14) Legs without well developed coxal organs. (15) Crural glands absent. (16)* Accessory glands of the male open medianly and dorsally near the hind end. The interesting point about this species is that though occurring so near to Australia, it differs absolutely from Austro-Peripatus in the character of its ovum.

Capo-Peripatus. Natal and Cape Colony. Seven species are known. The characters are : (1) Number of legs (16-25 pairs) is variable when the number of pregenital legs exceeds 19 pairs. (2) Outer jaw with one minor tooth, inner jaw without diastema or saw. (3) Legs with 3 spinous pads. (4) Nephridial openings of legs 4 and 5 on the proximal pad. (5) Feet with 3 distal papillae, two anterior and one posterior, except in *cinctipes* in which the anterior papilla is dorsal; and except in *cinctipes* there are 2 papillae at the base of the feet (Fig. 336). (6) Genital opening between the legs of the last pair, which show a tendency to reduction and are sometimes obsolete (*P. capensis*). (7)* Receptacula seminis and ovorum absent except in *cinctipes* in which there is said to be a minute trace of receptacula seminis. (8) Ovary exogenous. (9)* Ova comparatively large and with but little yolk (.56 in greatest diameter in *capensis*, .4 mm. in *Balfouri*, probably about .2 mm. in *cinctipes*). (10)* Uterine embryos of nearly the same age; they differ most in *cinctipes*, in which however the difference is not very great. (11) Unpaired part of vas deferens short. (12) Spermatophores small, oval, with a thin coat. (13) Skin-pigment mainly blue, green, or black, not affected by spirit. (14) Coxal organs variable; usually not well developed; in *P. Sedgwicki* and *Moseleyi* they are moderately and in *P. cinctipes* well developed. (15) Crural glands present in most legs of both sexes, except possibly in *P. cinctipes*. (16) The accessory glands of the male open into the terminal part of the vas deferens, except in *P. cinctipes* in which they open separately between the anus

and the genital opening. The group is interesting for presenting a greater variation in structure than any other group. This variation reaches its maximum in *cinctipes* but is not sufficient in our opinion to justify the separation of this form from the rest. The following species may be mentioned: *P. capensis* Grube, with 17 (rarely 18) pairs of legs; *P. Balfouri* Sedgwick, with 18 (rarely 19) pairs; *P. Moseleyi* Wood-Mason, with 20–24 pairs; and *P. (Opisthopatus) Purcell* *cinctipes* Purcell with 16 pairs.

Austro-Peripatus. Australia (W. and E.), Tasmania, New Zealand. Eight species are known. The characters are: (1)* The number of legs (14 to 16 pairs) is constant in the same species. (2) Outer jaw without minor tooth or with one or more minor teeth; the inner jaw is without a diastema or saw of denticles. (3) The legs have 3 spinous pads. (4) Nephridial openings of legs 4 and 5 on the proximal pads. (5) Feet with 3 distal papillae (one anterior, one dorsal, and one posterior), except in *P. Suteri* in which there may be 3 or 4. (6) The genital opening is between the legs of the last pair which are normally developed. (7) The oviduct has a receptaculum seminis with 2 ducts, but has no receptacula ovorum. (8) Ovary is exogenous. (9) Ova very large (1.5 to 2 mm. in longest diameter) and heavily yolked. (10) Uterine embryos of very different ages or about the same age. (11) Unpaired part of vas deferens long. (12) Spermatophore elongated, with a thick case. (13) Skin pigment mainly black, blue, green, or brown, unaffected or but slightly affected by spirit. (14) Legs without well developed coxal organs. (15) Crural glands present in some species, absent in others; when present, in the males only. (16) Accessory glands of the male opening separately between the anus and genital opening. On the whole this group of species, which has a considerable range, presents but little variation. There is a little variation in the outer blade of the jaw, in the pedal papillae, in the relative ages of the embryos in the same uterus, and in the crural glands. Also in 3 species the oviduct opens at the end of a papilla—the ovipositor. This character is associated in two of the three species (and possibly in the third) with an oviparous habit and a sculptured egg-shell. The only peculiar character is No. 1. The other characters are distributed fairly impartially among most of the other groups. If we are inclined to associate *Austro-Peripatus* with *Melano-* and *Capo-Peripatus* we must not overlook the important characters Nos. 1, 9 and 11 by which it differs from them.

Chilio-Peripatus. Chili, 1 species, *P. Blainvillei*. Though this species is South American it occurs far to the south of any *Neo-Peripatus* and is entirely distinct from that group. Its characters are: (1) Number of legs (19–21 pairs) variable in the species. (2) Outer jaw with 2 minor teeth, inner jaw without a diastema and saw. (3) Legs with 3 spinous pads. (4) Nephridial openings of legs 4 and 5 on the proximal pad. (5) Feet with 3 distal papillae (one anterior, one posterior, and one dorsal). (6) Genital opening between the legs of the last pair which are reduced in size. (7) Receptaculum seminis, if present, very much reduced, without double duct; no receptacula ovorum. (8) The ovary is endogenous. (9) Ova small (.07 mm.), but not so small as in *Neo-Peripatus*. (10)* Uterine embryos of markedly different ages, but arranged in groups of three, the embryos of each group being of the same age. (11) Unpaired part of vas deferens short as in *Capo-Peripatus*. (11a)* A part of the vas deferens on each side is coiled into a close spiral. (12) Spermatophores are small and cylindrical, without a specially thick case.

(13) Skin-pigment green or black with reddish patches, but little affected by spirit. (14) Without well developed coxal organs. (15) Crural glands unknown. (16) Accessory glands of male unknown. This species is specially interesting, because, while occurring so near Neo-Peripatus and resembling it in two important characters found nowhere else (endogenous ovary and small ovum), it differs from that group in most of its characters and approaches Capo- Austro- and Melano-Peripatus. But it possesses two important peculiar features (Nos. 10 and 11a). In our opinion the association of this species with the Cape species *P. cinctipes* in Purcell's genus *Opisthopatus* is inadmissible. The discovery by Bouvier of the characters of Chilio-Peripatus is the most important which has been made since Evans discovered and described Eo-Peripatus.

The important lessons which the distribution of the species of Peripatus teach are, (1) the geographical groups of species are natural zoological groups, (2) the distinguishing specific characters are distributed in a haphazard manner in the different groups, so that it is quite impossible to show the phylogenetic affinities of the species by a genealogical tree.

CHAPTER VII.

CLASS III. MYRIAPODA.*

Tracheates with numerous and similar pedigerous segments, with one pair of antennae followed by a pair of palpless mandibles, with regularly and segmentally arranged tracheal stigmata, and with malpighian tubules. The young are, with a few exceptions, not provided with the full complement of segments at hatching.

Very few of the characters mentioned in the definition are peculiar to Myriapoda; they are almost all found in Insecta or Onychophora. This fact coupled with the great variation of structure found in the group points to the conclusion that the classes Insecta, Onychophora and Myriapoda are the survival of a once great and continuous group of land Arthropods, a large number of which have become extinct, leaving two groups, Insecta and Onychophora, each fairly compact and showing but little variety of organization, and one, the Myriapoda, loose and heterogeneous with considerable gaps between the orders. In fact it might fairly be held, and has indeed been maintained, that the line of cleavage between the opisthogoneate and progoneate Myriapoda is sufficiently distinct to justify the abandonment of the class and the substitution in its place of two classes, the *Opisthogoneata* including the Chilopoda, and the *Progoneata* with the Chilognatha, Pauropoda, and Symphyla as orders. Of these two classes the Progoneata have special features of their own, *e.g.* the position of the genital opening

* J. F. Brandt, *Recueil des mémoires relatifs à l'ordre des Insectes Myriapodes*, Petersbourg, 1841. G. Newport, On the nervous and circulatory systems of Myriapoda and Macrourous Arachnida, *Phil. Trans.* 1843. M. Fabre, Recherches sur l'anatomie des organes reproducteurs et sur le développement des Myriapodes, *Ann. Sci. Nat.* 1855. C. L. Koch, *Die Myriapoden*, 2 Bde, Halle, 1863. H. Grenacher, Ueber die Augen einiger Myriapoden, *Arch. f. Mikr. Anat.*, 18, 1880. R. Latzel, *Die Myriapoden der österreichisch-ungarischen Monarchie*, 1 and 2, Wien, 1880, 1884. A. Kowalewsky, Étude des glandes lymphatiques de quelques Myriapodes, *Arch. Zool. Expér.*, 1896. Also E. Ray Lankester, R. Heymons, *op. cit.* on p. 314.

and of the gonad, the diplopody, the number of the jaws, which give them strong claim to independence; while the Opisthogoneates in the features mentioned present a distinct approximation to Insecta, from which they principally differ in the number and uniformity of the segments and in the absence of a differentiated thorax and abdomen. And there would be a strong case for this grouping, were it not for the Symphyla, which, although progoneate and agreeing with the Pauropoda in the non-correspondence of the legs and the sterna, resemble Chilopods in the presence of a ventral blood-vessel, in the absence of diplopody, in the width of the sternal plates, and in the arrangement of the jaws. In fact in the latter point they may be said to be more insectan than the Chilopoda. Having regard to these facts, it seems unsatisfactory to place the Symphyla with the Diplopoda (Chilognatha) and Pauropoda as Progoneates. On the other hand it is impossible to place them with the Insecta from which they differ in their progoneate condition (a feature to which considerable morphological importance is attributed), and in their numerous segments and in the absence of a differentiated thorax and abdomen. The only other course open to us is to retain the old group Myriapoda and to leave them in it, indicating their insectan affinities by placing them next the Chilopoda. This is the course we have followed in this work: we have retained the class Myriapoda and divided it into four orders, the *Pauropoda*, the *Diplopoda*, the *Chilopoda*, and the *Symphyla*. We admit the interdigitation of these orders with each other and with the class Insecta, and we think that there are good reasons which would entirely justify the revival of the class *Antennata* to include them. We do not here establish such a class mainly on the grounds of convenience and recent custom. If we did, we should define it as follows: *Tracheates with antennae, with more than one pair of jaws, with malpighian tubes and definite metameric stigmata*; and we should divide it into five orders, viz., *Pauropoda*, *Diplopoda*, *Chilopoda*, *Symphyla*, and *Insecta*.

The consideration of the Pauropoda still remains. They might be united with the Diplopoda. We prefer however to keep them apart, on the ground of the fewness of their segments, the incompleteness of their diplopody, the width of their sternal plates, and the dorsal position of the testis (not of the

ovary). Their Diplopod features are : their progoneate condition, the number of their jaws, the form of their larva, and their incipient diplopody.

Of all the characters mentioned in our definition, the only one which is peculiar to the class is that referring to the number of legs and segments in the young at hatching, and even that is not found in all Myriapods, a few of the Chilopoda being hatched with the full number of segments and appendages.

It will be observed that we make no attempt to bring the head of the Diplopoda and Pauropoda into line with the general scheme given on p. 325. In spite of recent work (*see note p. 589*) we do not think that this can at present be done with any advantage to Science.

Myriapoda make their appearance in the Carboniferous in form not very different from those now living.

Order PAUROPODA *

Minute progoneates with a head bearing three pairs of appendages (antennae, mandibles and maxillae) and with twelve trunk-segments, nine of which bear legs.

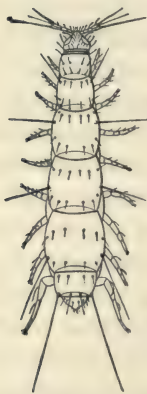


FIG. 346.—*Pauropus Huxleyi* (after Latzel).

The Pauropoda are small myriapods, less than two mm. in length. They possess a distinct head and a body in which indications of twelve segments, carrying in all nine pairs of legs, can be made out (Fig. 346). The head carries a pair of triflagellate antennae, a pair of mandibles, and a pair of weak maxillae united to form an underlip (hypostoma). It is without eyes, though on each side of it there is a large eye-like surface which however is

devoid of ocular structure. The antennae possess a four-jointed base with two branches, of which the dorsal bears

* Lubbock J., On *Pauropus*, a new type of centipede, *Trans. Lin. Soc.*, 26, 1866, p. 181. Latzel R., *op. cit.* Schmidt P., Beiträge zur Kenntniss der niederen Myriapoden, *Z.f.w.Z.*, 59, 1895, pp. 436–507. Kenyon F. C., Morphology and Classification of the Pauropoda, *Tuft's College Studies*, 4, 1895, pp. 77–146. Hansen H. J., On the genera and species of the order Pauropoda, *Vid. Medd. Naturh. For.* Kopenhagen, 1901, pp. 323–424. Silvestri P., Ordo Pauropoda, in A. Berlese *Acari, Myriopoda, et Scorpiones hucusque in Italia reperta*, 1902.

one flagellum, and the ventral two flagella and the so-called *globulus*. The flagella are ringed and the globulus, which may be stalked or sessile, is probably a sense organ. There are six well-marked tergal plates (except in the *Brachypauropidae*): of these each of the first five lies over two segments, while the last is the tergum of the legless preanal segment. In addition there is the anal segment with a tergum of its own, which may be covered by the tergum of the preceding segment. The appendages of the first segment are stump-like and small. The other trunk appendages (nine pairs) are legs which are set wide apart on the sterna and terminate in claws; the first and last pairs of these are five-jointed, the remainder being usually six-jointed. There are five pairs of long tactile hairs which project from the sides of the body beneath the second to the sixth tergal plates. The adult males have copulatory organs at the base of the legs of the third pair (counting the reduced legs as the first).

The alimentary canal consists of a short foregut (oesophagus), a long dilated midgut, usually receiving at its hind end two malpighian tubes (absent in *Pauropus* * etc.), and of a short conical rectum with a chitinous lining. The anus is at the end of the anal segment. There are three pairs of salivary glands opening into the inner part of the mouth. The brain is large and fills up the greater part of the head, and the ventral cord possesses nine ganglia. There is no distinct body-cavity but the space between the organs is occupied by a fat-body composed of large cells. Heart and blood-vessels are absent.

Special respiratory organs appear to be almost completely absent. The only traces of them are two very fine, structureless tubes opening on the head at the base of the mandibles and not extending back beyond the first body segment. These are interpreted by P. Schmidt as tracheae. They are without nuclei in their walls. The general integument, which is remarkable for its thinness, must serve as a respiratory surface.

The female genital organs consist of an unpaired ovary, oviduct, and receptaculum seminis. The ovary is a longish tube lying ventral to the gut and extending from the fourth to the eighth segment. The single oviduct opens behind the second pair of fully developed legs in the middle line. The receptacu-

* Absent elsewhere in Tracheates in *Japyx*, *Peripatus*, *Collembola* and some *Arachnids*.

lum seminis opens with the oviduct. The male organs consist of an unpaired testis placed dorsal to the gut and sometimes partly or completely divided into two or more portions, and of paired, somewhat complicated ducts, which are united by connecting canals and which open separately on the segment of the second pair of fully developed legs through the copulatory processes there found.

Very little is known of the development. The just-hatched young possess three pairs of legs and they attain the adult condition by a series of moults. They can elongate and shorten their bodies by contraction to a considerable extent. They avoid light, living beneath objects (stones, wood, etc.) in damp places. The more active forms prey on other microscopic animals, and those which are more sluggish eat decomposing animal and vegetable substances.

The Pauropoda appear to represent a primitive group of Myriapoda, with affinities to the Diplopoda by the incipient diplopody shown in the relation of some of the terga to the leg-bearing segments, by the number of the jaw-appendages, by the condition of the just-hatched young, by the unpaired gonad, and the position of the genital opening. On the other hand in the dorsal position of the testis they present a feature of similarity to the Chilopoda.

Fam. 1. **Pauropidae.** Head free and uncovered; with rounded bodies, long legs and agile movements. The trunk has 6 terga, feebly chitinized, and the anal segment which is uncovered dorsally. The integument is white and smooth. World-wide. *Pauropus* Lubbock (Fig. 346), more than 21 species, *P. Huxleyi* Lubbock, British. *Stylopauropus* Cook, *S. pedunculatus* Lubbock, British.

Fam. 2. **Brachypauropidae.** Head free and uncovered. Terga of the trunk consist of nine pairs of plates and an unpaired plate, all fairly chitinized. Movement slow. *Brachypauropus* Latzel, Austria and Italy.

Fam. 3. **Eurypauropidae.** Head concealed beneath the first tergal plate; with depressed bodies, short legs and slow movement; trunk with 6 terga, firmly chitinized. The anal segment is hid beneath the produced 6th tergum. *Eurypauropus* Ryder, N. Amer., Austria, Italy.

Order DIPLOPODA *

Progoneates with a head bearing two pairs of jaws (mandibles and maxillae), a thorax consisting of four segments and usually

* Latzel R., *Die Myriopoden der Österreichisch-ungarischen Monarchie*, Zweite Hälfte, Wien, 1884. Silvestri F., *J. Diplopodi*, Genova, 1896. Id., *Classis Diplopoda*, vol. 1, Portici, 1903. E. Metschnikoff, *Embryologie*

bearing three pairs of legs, and a body consisting of numerous, for the most part double segments. The gonad is ventral to the gut and its ducts open on the second or third post-cephalic segment.

The body is, as a rule, cylindrical or sub-cylindrical (Fig. 356), but sometimes it is flattened dorsoventrally. It frequently possesses the power of rolling itself into a spiral or ball. In many forms it is much elongated, but in the Oniscomorpha (and Limacomorpha) the body is almost as broad as it is long. The length varies from 2 mm. in *Polyxenus* to upwards of 200 mm. in some tropical Julidae (*Rhinocricus*, *Spirostreptus*). The chitinous exoskeleton is hard (except in *Pselaphognatha*) owing to the presence of calcareous salts, but after moulting it is soft and usually paler. The head (see p. 589) carries only three pairs of appendages, the antennae, mandibles, and the maxillae which are applied together to form a *gnathochilarium* (or hypostoma). The antennae are in general short and club-shaped, and consist usually of seven segments, of which the last is often concealed in the penultimate piece and almost always bears four spines. The eyes, which are aggregated and simple eyes, are placed behind the antennae at the sides of the head, more rarely on the middle of the forehead. They may be completely absent, although the forms in which this occurs do not differ in habits from those in which they are present. They are usually numerous, but may be reduced to 5, 3, or even 1 on each side. Between the eyes and the antennae there is a small pit which may be provided with a projecting hair.

The labrum (upper lip) is continuous with the front of the head (clypeus) and usually bears three teeth. The mandibles (Fig. 347) are palpless, and consist of a stem (stipes mandibularis, *sti*) and a distal portion (*ma*) which carries a powerful movable tooth (*de*) and a plate with a broad masticatory surface provided with toothed ridges (*lp*). The gnathochilarium (Fig. 348) is

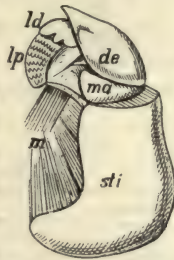


FIG. 347. — Right mandible of *Glomeris conspersa* (after Latzel). *de* the large tooth; *ld* the toothed plate; *lp* the toothed ridges (laminae pectinatae); *ma* distal portion of the stem (mala mandibularis); *m* muscle; *sti* stipes.

der doppelfüssigen Myriopoden, *Z.f.w.Z.*, 24, 1874. F. G. Heathcote, The early development of *Julus terrestris*, *Q.J.M.S.*, 25, 1883. Id., The postembryonal development of *Julus terrestris*, *Phil. Trans.*, 1888.

formed by the junction of the second pair of mouth parts (maxillae) which in early life are distinct. It strongly recalls the labium of insects, with which however it can hardly be homologous,

(see table of comparison p. 325). It consists of a more or less flat plate which forms a lower lip and shows a number of different parts marked off from one another more or less perfectly by thin seams in the chitin. Except in the Polyxenidae and Polyzonidae, in which the gnathochilarium is degenerate, the parts shown in Fig. 348 may be made out. Of the post-cephalic segments, two are specially varied in form, viz., the collum or neck

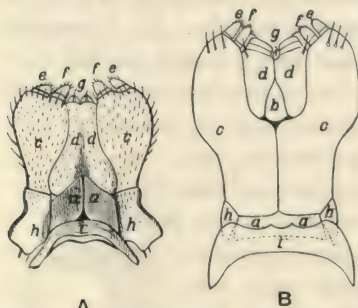


FIG. 348.—Gnathochilarium, *A* of *Glomeris*, *B* of *Julus* (after Latzel). *h* Hypostoma (basilare); *a* mentum (infrabasilare); *b* promentum; *d* lingua; *g* lobi linguales; *h* cardo gnathochilarii; *c* stipites gnathochilarii; *e* mala gnathochilarii exterior; *f* mala gnathochilarii interior.

segment, which comes next behind the head, and the anal segment. The collum varies much in the size and shape of its tergal plate. In the Platydesmidae it is larger than the head, in Polyzonidae it is semielliptical, in Pselaphognatha it is small and narrow, in Chordeumidae it is elliptical and convex, and in the Polydesmidae it is of every variety of shape and size. The anal segment is larger than the others and in many species its tergum is prolonged into a spike which serves as a specific character.

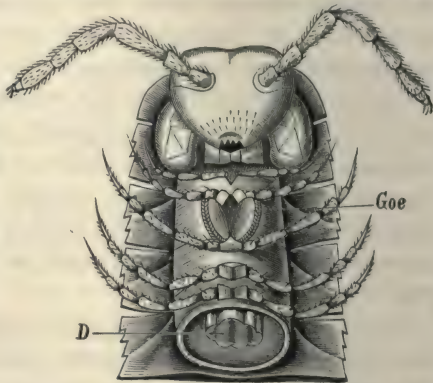


FIG. 349.—Ventral view of head, thorax, and first double segment of a female *Polydesmus complanatus* (after Latzel). *Goe* female generative opening; *D* alimentary canal.

The first four segments (Fig. 349) which may be regarded as a kind of thorax, carry only three pairs of appendages amongst them, one being apodal. From the fifth segment (in the Polyzonidae from the fourth) each segment carries

two pairs of legs. An exception to this is formed usually by the last three segments and in the sexually mature male by the seventh segment, these being apodal or with one pair of legs only. The number of segments varies from 100 or more in the elongated Polyzonidae and Julidae to less than 25 in the Polyxenidae and Glomeridae. It may vary in the same species, or the number may be constant, the limit of growth in this respect being presumably attained at a comparatively early period of life.

In most forms the anterior part of each segment is narrower than the posterior and penetrates a little way into the segment in front of it in a telescopic manner. The segments carrying two pairs of legs are to be regarded as having arisen by the fusion of two segments (p. 589), a trace of this union being often present as a transverse furrow which marks them into an anterior and posterior portion.

Each segment is covered by definite chitinous plates. There is an arched plate the *tergite* (tergum), usually single, which covers the back and extends on to the sides. There are two lateral pieces, the *pleura*; and one or two pairs of ventral plates, the *sternites* (laminae pedigeræ), which carry the legs and the tracheal openings. The sternites may be united across the middle to form a single plate (Polydesmidae). These plates may be separate and movable upon one another, or they may be partly united with each other, or completely united to form a continuous ring. The last segment consists of a tergite, an unpaired anal plate (? sternite) and two anal valves which enclose the anus.

The legs have normally 6 or 7 joints, named as follows : coxa trochanter, femur, tibia, tarsus 1, tarsus 2, tarsus 3; tarsus 3 carries a claw. They have approximately the same size and shape. The legs of a pair are usually attached close together to their sternite, but sometimes they are widely separated (Pselaphognatha). In the male the legs of the first postcephalic segment are modified (hooklike) in connexion with copulation. On the seventh segment, and sometimes on the sixth and eighth (in *Glomeris* on the penultimate segment) there is in the male a complicated apparatus which may replace either one pair or both pairs of legs and is known as the auxiliary copulatory apparatus. It has been regarded as the modified legs of the

segment, but inasmuch as it may coexist with both pairs of legs (Callipodidae) it is regarded by Silvestri as an organ sui generis. It consists usually of two pairs of leg-like processes and is used for transferring the sperm to the vulva of the female in copulation. In the female this apparatus is absent and the legs of the segment concerned are normally present. The variations presented by the auxiliary copulatory apparatus are of considerable importance in the classification.

In all Diplopods the genital openings are paired and placed in both male and female, on the ventral surface between the 2nd and 3rd pairs of legs either between the 2nd and 3rd segment or on the 3rd segment, or on the coxae of the legs of the 2nd pair. In the male there is often a freely-projecting double penis at the end of which the opening is placed. The penis is not apparently used in the sperm transference (except possibly in the Polyxenidae); this being effected by the above mentioned copulatory appendages which are actually inserted into the vulva.*

The alimentary canal consists of a narrow oesophagus (stomodaeum), into which, at the base of the gnathochilarium, open the two salivary glands; a midgut or intestine (mesenteron) which is a wide tube beset with short liver diverticula and often presents transverse marks which correspond with the segments; and a hind gut (proctodaeum), which receives at its junction with the midgut two or four malpighian tubes. In *Glomeris* the intestine is slightly curved.

In the central nervous system, the nerves to the jaws are given off by the suboesophageal ganglion. The ventral nerve-cord extends the whole length of the body. Its ganglia are more or less approximated; but each double segment possesses two, and the ganglia of the first three postcephalic segments are more closely united than the others, though there is not the same degree of differentiation into a thoracal and abdominal nervous region that is found in the Chilopoda.

The special sense organs are represented by the aggregated simple eyes (p. 329), by the olfactory hairs on the antennae and a tuft on the gnathochilarium, and by the organ of Tömösvary

* Fabre (*Ann. Sci. Nat.* (4), Zool., 3, 1855) states that in Polyxenidae and Julidae copulation takes place in September in captive animals, and that light has a powerful influence in bringing it on. Sinclair has observed it in May in Julidae, and in June in Polydesmidae.

which consists of a transparent projection of chitin covered with fine sensory hairs and placed on the head near the base of the antennae. The hypodermis cells below the projection are specially modified and supplied by a special nerve from the brain.

The vascular system consists of a dorsal tubular heart contained in a pericardium and branching into arteries in the head. In each double segment there are two pairs of ostia, one at each end of the segment, and it gives off from the middle of each segment two (or one) pairs of arteries which pass into the fat-body.

The **tracheae** are unbranched in most Diplopods, but in the Oniscomorpha they are branched. They arise in tufts from tracheal pouches which open on the sternites immediately in front of the articulation of the legs. There are therefore two pairs of stigmata in each double segment and one pair in the others. There are two kinds of tracheae: some larger and with distinct spiral fibres, others smaller without the spiral fibre. In some Diplopods both kinds are present; in others, one or the other kind only.

The **excretory organs** are represented by two or four malpighian tubes which open into the gut at the junction of the intestine and hind gut. It is possible that the cells of the fat-body which contain urate of soda have also to do with excretion. It has also been suggested * that the salivary glands, which as Heathcote † has shown develop in *Julus* by the direct transformation of a portion of the mesoblastic somite of the segment of the gnathochilarium, may have the physiological as well as the morphological characters of nephridia.

The *glandulae odoriferae* are placed laterally, one pair in each segment; they open on the sides of the body by the foramina repugnatoria which were formerly mistaken for tracheal stigmata. In the Oniscomorpha the openings of the glands of the two sides are united, so that there is only one row of foramina repugnatoria placed in the dorsal middle line. They begin usually in the 5th or 6th segment and are not found in the apodal segments. The secretion is often evil-smelling and contains prussic acid.

* Bruntz L., Contribution à l'étude de l'excretion chez les Arthropodes, *Arch. Biol.*, 20, 1903, p. 217.

† *Phil. Trans.*, 1888, p. 160.

The generative glands (Fig. 350) are unpaired elongated tubes, the paired ducts of which open (p. 586) on the 2nd or 3rd body segments. They are placed on the ventral side of the gut and develop, as in *Peripatus*, from the dorsal divisions of the embryonic somites (Heathcote).

All Diplopoda are, so far as is known, oviparous. The eggs are laid, shortly after copulation, in masses in damp earth, under stones, etc. Sometimes a kind of nest is made, and in some species the mother keeps watch over the eggs (*Julus*, *Polydesmus* etc.).

Development.* The ovum is of fair size and contains a

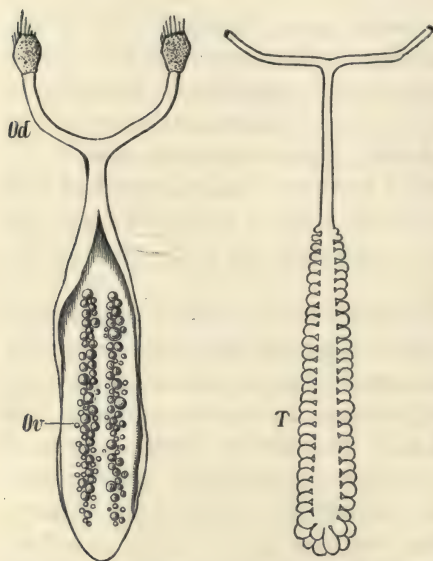


FIG. 350.—Generative organs of *Glomeris marginata* (after Fabre). T testes; Ov ovary; Od oviduct.

considerable quantity of yolk. The nucleus of the unsegmented zygote lies in the centre of the ovum in a little protoplasm. It here divides by a series of binary divisions, each product being surrounded by a little protoplasm. When a certain number of nuclei have been formed, some of them with their protoplasm migrate to the surface and form outside the ovum a nucleated layer which

constitutes the blastoderm and gives rise to

the ectoderm. The yolk usually becomes divided at about this period into pyramids which give a superficial aspect of complete cleavage, but it is not clear that each of these contains a nucleus. The blastoderm acquires a keel-like thickening over part of its extent. The mesoderm bands are derived from this. The nuclei which remain in the yolk give rise to the endoderm, and possibly some of them may apply themselves to the keel and participate

* Korschelt and Heider, *Textbook of Embryology of Invertebrates*, English Translation, vol. 3, 1899, Swan Sonnenschein & Co., where the literature to date will be found. F. G. Heathcote, *op. cit.* E. Metschnikoff, *Embryologie der doppeltfüssigen Myriapoden*, *Z.f.w.Z.*, 24, 1874.

in forming the mesoderm. Well-marked mesoblastic somites are formed. These become hollow and extend into the appendages, the first being in relation with the antennae, the second with the mandibles, the third * with the maxillae (gnathochilarium), and so on, each double segment containing, as was shown by Heathcote, two pairs of somites. The somites, as in *Peripatus*, divide into one part which remains in the appendage and, becoming solid, gives rise to muscles, and into a part which remains in the body. This part in some segments (antennal, mandibular, etc.) becomes solid and its walls transformed into muscles, etc.; in others it approaches its fellow between the gut and the nerve-cord and, fusing with it and with the corresponding structures of adjacent somites, gives rise to the reproductive gland. In the segment of the gnathochilarium, this body-part of the somite remains distinct from its fellow and gives rise to the salivary gland. The yolk lies outside the enteron in the haemocoel (Fig. 351). The oesophagus and rectum (hind-gut)

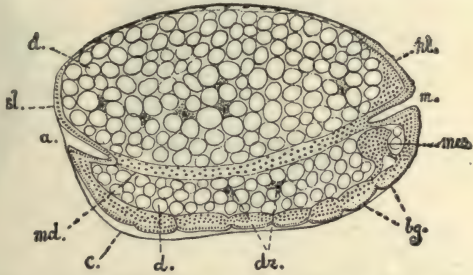


FIG. 351.—Longitudinal section through an embryo of *Julus terrestris* on the tenth day of development (after Heathcote), showing the solid string of endoderm which will give rise to the mesenteron. *a* Anus; *bg* ventral ganglia; *c* cuticular envelope of embryo; *d* yolk; *dz* yolk cells; *kl* cephalic lobe; *m* mouth; *md* enteron; *mes* mesoderm; *sl* caudal lobe.

arise as epiblastic ingrowths, and the malpighian tubes are outgrowths of the hind-gut. An embryonic cuticular envelope is formed by the ectoderm at an early stage (in *Julus* before the segmentation of the germ-band), and a second one later on.

* M. Robinson (*Q.J.M.S.*, 51, 1907, p. 607) has recently asserted that in the embryonic development of an African Diplopod (*Archispirostreptus*) there is evidence of a tritocerebral (preantennary) and of a maxillular (1st maxilla) segment. If this contention is a sound one it will enable us to homologise the gnathochilarium with the 2nd maxillae and will bring the head of Diplopods into harmony with that of Chilopods (*see* table on p. 325). The evidence, however, is unsatisfactory. It consists of obscure indications of embryonic ganglia, which, unless supported by evidence of mesoblastic segments, is very unreliable in deciding questions of this kind. There does not appear to be any embryonic evidence in favour of the view held by some that the gnathochilarium consists of two pairs of appendages, the so-called "postmaxillary segment" of the embryo being the first body segment.

These must be looked upon as being due to two precocious ecdyses. In some cases the embryo remains within the embryonic cuticle for a short time after hatching (*Julus*, *Polydesmus*, *Strongylosoma*), and a kind of resting pupal stage is passed through; but in all, the larva, when it becomes free and active, has three pairs of legs (Fig. 352) and a certain number, usually four, of apodal segments behind. It thus presents a superficial

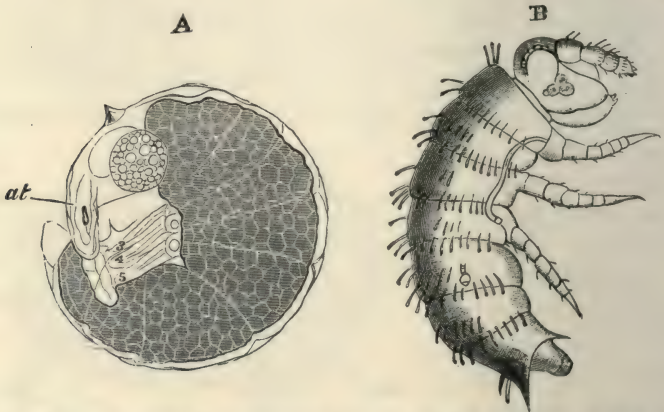


FIG. 352.—Two larval stages of *Strongylosoma Guerinii* (after Metschnikoff). In A the larva is still surrounded by the cuticular envelope which bears the egg-tooth; in B it has shed this envelope and has entered upon its free life. at antenna, above and posterior to which the egg-tooth can be seen; 3, 4, 5 the three pairs of legs.

resemblance to an apterous insect. The three pairs of legs are attached to three of the first four body-segments, usually the first, third or fourth (Fig. 353). Moreover some of the apodal posterior segments possess the rudiments of legs beneath the cuticle. The larval development takes place gradually (so-called anamorphosis) and consists mainly in the increase in the number of antennal joints, of ocelli, and of the segments and appendages. The segments are added between the anal segment and the segment in front of this, either one double segment at a time, or in groups of two, three, or even more.

In *Glomeris*, the just-hatched larva has five pairs of rudiments (freely projecting) of legs behind the three pairs of functional legs. In *Polydesmus** in which the functional legs are on the first, third and fourth (Fig. 353)

* There is some conflict of evidence as to which is the apodal segment. It appears certain (Sinclair) that in the embryo of *Julus* and *Polydesmus* the first post-cephalic segment is apodal, and that the first pair of legs shift forward in early larval life, leaving the second apodal.

trunk segments, the fifth segment bears two pairs of rudimentary legs beneath the integument, and the sixth has one pair. In *Julus* the just-hatched larva is very similar to that of *Polydesmus*. In the species in which the number of segments in the adult is constant, sexual maturity with development of the copulatory limbs is attained after the formation of the full number of segments. In forms in which the number of segments is inconstant it would appear that formation of new segments must take place after attainment of sexual maturity.

The Diplopods are sluggish animals and live mainly on vegetable substances; some devour animal excrements, and a few are, occasionally at least, carnivorous. They avoid the light and live in damp places under stones, etc. They are useful in nature in helping to destroy decomposing organic matter, and some species (e.g. of *Julus*) are known as wire-worms. They are found all over the world, but the largest and most striking species are tropical.

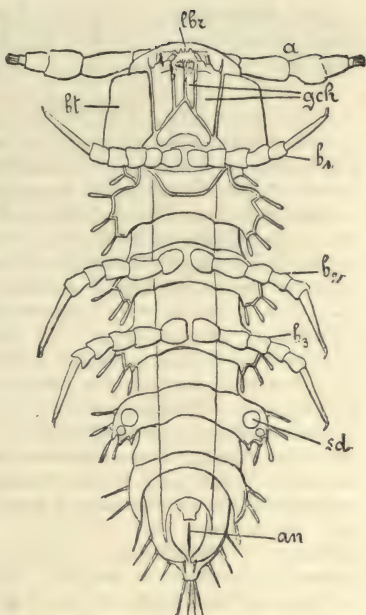


FIG. 353.—Newly hatched larva of *Polydesmus complanatus* (after vom Rath). *a* antenna; *an* anus; *b₁-b₃* the three pairs of legs; *bt* sides of the head; *gch* gnathochilarium; *lbr* labrum; *sd* glandula odorifera.

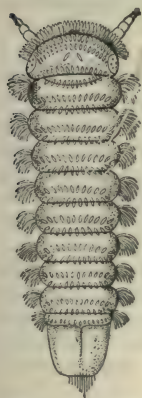


FIG. 354.—*Polyzenus lagurus* (after Latzel).

Sub-order 1. *Pselaphognatha*.*

Small Diplopods with soft chitin without calcareous deposit, with 10–12 body segments carrying 13 pairs of legs, with toothed hairs in tufts on the pleura and in transverse rows on the terga (Fig. 354), without foramina repugnatoria (glandulae odoriferae). The labrum is free; the mandibles are buried in the mouth-cavity and rub against the roof of the mouth which is armed with teeth; the maxillae are reduced, consisting of little more than a pair of palps attached to a basal plate. The male is without the copulatory appendages, and the anus is in the penultimate segment. The coxae of the legs are widely separated from one another and there is a well-developed sternal region. Europe, Asia, America.

* Latzel, *op. cit.*, 2, p. 69. F. G. Sinclair, *Q.J.M.S.*, 30, 1889, p. 87.

Fam. **Polyxenidae**. *Polyxenus* Latreille, pursues and destroys the vine-louse (*Phylloxera*); Central and S. Europe, England. *P. lagurus* L. (Fig. 354).

Sub-order 2. **Chilognatha**.*

The chitinous covering of the body is hardened by calcareous salts. The labrum is fused to the cephalic shield and glandulae odoriferae are present. The mouth parts have the form described for the order, and consist of a pair of mandibles and a pair of maxillae (*gnathochilarium*). The males always possess one or two pairs of copulatory appendages on the last segment or on the 7th or on the 7th and 8th (according to Silvestri these appendages are not modified legs and may or may not coexist with the ordinary appendages). The anus is on the last segment.

Tribe 1. *Oniscomorpha*. The body is short, strongly convex dorsally and capable of being rolled into a ball; body segments 11–13 in number; foramina repugnatoria in a single, median dorsal row, beginning in the 4th segment. Pleura and laminae pedigeræ free. Genital apertures at the base of the legs of the 2nd pair. No penis; the copulatory appendages are on the penultimate segment, which also bears one pair of legs. Segments 1, 2, 3, and 4† and the penultimate (and in the male the antepenultimate) have one pair of legs, the other segments, except the last, have two pairs.

Fam. 1. **Gervaisidae**. Antennae approximated at their bases and placed on the front of the head, eyes in a row at the sides of the head, 11 tergites, the infrabasal (mentum) of the *gnathochilarium* undivided. *Gervaisia* Waga, palaearctic region.

Fam. 2. **Glomeridae**. Antennae and eyes as in the Gervaisidae, 12 tergites, infrabasal divided. *Glomeris* Latr., palaearctic and Indo-malayan (Fig. 355).

Fam. 3. **Sphaerotheridae**. Antennae apart at the base, at the sides of the head; eyes in several rows; 13 tergites; infrabasal undivided. *Sphaerotherium* Brandt, Asia, Africa, Australia. *Zephronia* Gray.

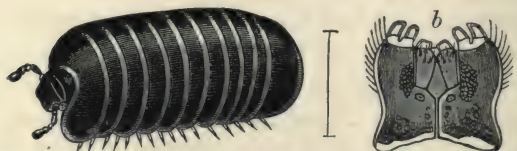


FIG. 355.—a *Glomeris marginata* (after C. L. Koch), b maxillae (*gnathochilarium*) of *Julus terrestris*.

The family **Glomeridesmidae** (Sumatra and C. Amer.) closely similar to the above, but with 19–20 segments and without foramina repugnatoria, has been placed in a tribe *Limacomorpha*

distinct from the *Oniscomorpha*.

Tribe 2. *Helminthomorpha*. Body usually elongated, more or less cylindrical, rollable into a ball or spiral. Segments 19 to 108. Foramina repugnatoria placed on the sides of the body. Pleura free or fused with tergites. Laminae pedigeræ free or fused with pleura. Copulatory appendages on segments 7 and 8, or 6, 7 and 8; legs in these segments present or absent.

Fam. 1. **Callipodidae**. Eyes in several rows; pleura united to tergites,

* Latzel, Silvestri, *op. cit.*

† Pocock, *Zool. Ergeb. einer. Reise in Ost-Indien* (M. Weber), p. 322.

segments 1, 2, and 4 with one pair of legs, the third and the last three are apodal; no penis; copulatory appendages in anterior part of 7th segment, which is provided with two pairs of legs. *Spirostrephon* Brt., palaeartic and nearctic; *Callipus* (*Lysiopetalum*) Risso, palaeartic.

Fam. 2. **Chordeumidae** (*Chordeumoidea*). Body cylindrical or slightly depressed, attenuated in front and behind. Labrum with 3 teeth, mandibles with 9–12 combs. Pleura united with tergites. Laminae pedigeræ free. No foramina repugnatoria. Segments 30 or 32, constant. The third and two last segments apodal, the 1st, 2nd, 4th and antepenultimate with one pair of feet each, copulatory appendage in segment 7, or 6, or 8; no penis. *Trachysoma* Attems. *Atractosoma* Fanzago. *Craspedosoma* Leach. *Campodes* Koch. *Chordeuma* Koch. *Zygonopus* Ryder and *Scoterpes* Cope, eyeless, America.

Fam. 3. **Julidae** (*Juloidea*). With elongated usually cylindrical bodies, composed of a large number of segments (30–70 or more), which is variable within the limits of the same species. Eyes usually composed of numerous ocelli; many are blind. Labrum with 3 teeth, mandibles with cardo and from 4–10 combs. Pleura united with tergites; laminae pedigeræ (except the first two) united with the pleura, but with distinct suture, or free. The 3rd or 4th segments or none of the anterior segments are apodal, the last two segments are apodal. Foramina repugnatoria always visible in lateral series, usually beginning in 6th segment. Penis distinct; copulatory appendages on the 7th segment which is without legs. Cosmopolitan. *Cambala* Gray, N. America. *Nannolene* Bollman, N. and Central America. *Julomorpha* Porat, S. Afr. and Philippines. *Trachyiulus* Peters, Ceylon. *Spirostreptus* Brdt., Indo-Malaya. *Odontopyge* Brdt., Afr. and S. Amer. *Spirobolus* Brdt., Tropics. *Rhinocricus* Karsch, Australasia, S. Amer. *Julus* Brdt., Palaeartic; *J. terrestris* L.



FIG. 356.—*Julus terrestris* (after C. L. Koch).

(Fig. 356). *Blaniulus* Gerv., Palaeartic. *Unciger* Brdt. and *Pachyiulus* Berlese, Palaeartic. *Nemasoma* C. Koch, Palaeartic and Nearctic.

Fam. 4. **Polydesmidae**. Body more or less long, cylindrical or slightly flattened dorsally, without keels or with lateral horizontal keels which may be bent either towards the dorsal or ventral surface. Number of segments 19–20. Eyes always absent. Labrum with 3 teeth. Mandibles without cardo, usually with combs. Gnathochilarium with large, undivided infra-maxilla. Laminae pedigeræ in segments 2 and 3 free, rest united with pleura; pleura united with tergites. Foramina repugnatoria present in two lateral rows. First segment * and two last apodal, 2nd, 3rd and 4th each with one pair of legs (Fig. 349). No penis. Copulatory appendages on 7th segment, which has one pair of legs. Cosmopolitan, large forms from the tropics. *Sphaeriodesmus* Peters, Mexico. *Cyclodesmus* Hum-

* According to Silvestri. There seems however to be some doubt on the point, for according to some authors it is the 2nd segment which is apodal both in the larva and adult (Fig. 353).

bert and S., Mexico. *Cryptodesmus* Ptrs., Columbia. *Platyrhachis* C. Koch, Tropics except Afr. *Polydesmus* Latr., cosmopolitan. *Strongylosoma* Brdt., cosmopolitan. *Brachydesmus* Heller, 19 segments, Palaearctic.

The following three families are included by Silvestri with the Helminthomorpha, by Lätzel they are united in a distinct sub-order, the **Colobognatha**. They are small Diplopods with numerous segments (30–100), variable in the same species. Eyes present or absent. The small triangular head is elongated into a longer or shorter proboscis, and the mouth parts appear to be modified for suction, though it is doubtful if any, except those with long proboscis, are suctorial. The mandibles are small and the maxillae degenerate or absent. 3rd segment and two last apodal, 1st and 2nd with one pair of legs. Foramina repugnatoria present in two lateral rows. Copulatory appendages simple and in two pairs on the 7th segment, which is apodal. They live in damp places. Europe, Asia, America, Africa.

Fam. 5. **Siphonophoridae**. Head pyriform, produced into longish rostrum. Eyes and mandibles absent. Maxillae as a single lamina coalesced with labrum to form rostrum. *Siphonorhinus* Pocock, Malaya. *Siphonophora* Brdt., tropics.

Fam. 6. **Polyzonidae**. Head with short rostrum and eyes. Mandibles two-jointed. 2nd maxillae represented by a triangular plate. *Polyzonium* Brdt., palaearctic and nearctic.

Fam. 7. **Platydesmidae**.* Head small and spherical; eyes present or absent. Mandibles with 2 joints; maxillae as distinct gnathochilarium more or less reduced, inframaxilla undivided and long. Tergites with lateral keels. Segments numerous. *Platydesmus* Lucas, N. and C. America. *Dolistenus* Fanzago, Mediterranean.

Order CHILOPODA.†

Opisthogoneates with a head bearing three pairs of jaws (mandibles and two pairs of maxillae), a pair of poison claws (maxillipeds) on the first body segment, and with a body consisting of numerous segments, all of which, except the last two, bear one pair of legs. The gonad is dorsal to the gut and opens on the penultimate body-segment.

The body is flattened dorso-ventrally, and the legs are set far apart at the sides of the ventral surface. The chitinous covering is either very poor in, or completely free from calcareous salts, and in the course of life is frequently shed. The head,

* F. G. Sinclair, *Q.J.M.S.*, 49, 1905, p. 507.

† G. Newport, Monograph of the class Myriopoda, order Chilopoda, *Linn. Trans.*, 19, 1845. E. Metschnikoff, Embryologisches über Geophilus, *Z.f.w.Z.*, 25, 1875. N. Zograf, Anatomie v. Lithobius forficatus (Russian), *Schrift. d. Gesell. d. Freunde der Naturwiss.*, etc., Moscow, 1880. E. Haase, *Schlesiens Chilopoden*, Breslau, 1880–81. Id., Das Respirationssystem der Symphylen u. Chilopoden, *Schneider's Zool. Beiträge*, 1, 1885. R. Lätzel, *op. cit.* C. Herbst, Beiträge zur Kenntniss der Chilopoden *Bibl. Zool.*, 9, 1891. O. Duboscq, Rech. sur les Chilopodes, *Arch. Zool. Exp.*, 1898. R. Heymons, *op. cit.* on p. 314. C. Verhoeff, Chilopoden in *Bronn's Thierreich*, 1902–7.

which is covered by a cephalic plate (cephalite), carries four pairs of appendages, and the first segment of the body is in relation with the head by its appendages, the poison claws, which are called maxillipeds. The tergal plate of this segment is either absent, or weak, or well developed, in which case it is known as the basilar plate (*lamina basalis*). The segments behind this, except the two last, are much alike (*see below*) and each carries one pair of legs. The last two are apodal and bear, the first of them the median generative opening, the last the anus. In the Lithobiidae and Scutigerae some of the tergites are smaller than the others, and in the Craterostigmidae there are six tergites intercalated between the tergites of the pedigerous segments. The number of pedigerous body-segments varies considerably: the smallest number is 15 segments in Craterostigmidae, Lithobiidae, and Scutigerae, 21 in Scolopendridae, and from 30–173 in the Geophilidae. In the last-named family the number varies in different individuals of the same species. The number of leg-pairs is always unequal. The constitution of the head, in comparison with that of other Tracheates, is given in the table on p. 325 in the column for Myriapoda.

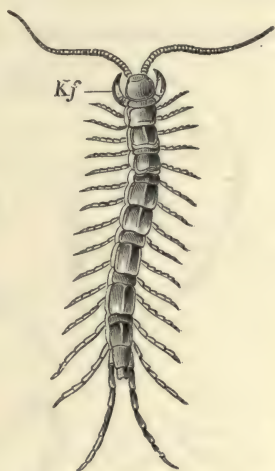


FIG. 357.—*Lithobius forficatus* (after C. L. Koch). *Kf*, poison claws (maxillipeds).

The antennae, which are usually set far apart, but in the Geophilidae are approximated, consist of from 12 to over 100 joints (when over 70 the segments are indistinct). Speaking generally their length may be said to vary inversely with that of the body. The eyes are ocelli: they are placed on the sides of the head behind the antennae and may be numerous or few or reduced to one pair (*Henicops*, and *Cermatobius*) or absent (*Geophilidae*, *Cryptops*, etc.). In *Scutigera* there is one pair of compound eyes. The labrum (Fig. 358, *Ob*) is either free or fused with the anterior and ventral part (*lamina frontalis*) of the cephalite. The mandibles (Fig. 358, *md*), which may present a division

into a basal (cardo) and peripheral (stipes) part, is without palps and bears at its end teeth (absent in some Geophilidae) and bristles. The 1st maxilla (Fig. 358, *Mx'*) consists of a shaft and two blades: the shafts of the two sides are approximated and may be fused. The 2nd maxilla (*Mx''*) consists of a basal piece, which is fused with its fellow to form a lower lip, and of a three-jointed leg-like palp which usually ends in a claw. This pair of appendages, from its resemblance to the 2nd maxillae of insects, is often called the labium. The maxillipeds or poison-claws (*Mf*) are the appendages of the first post-cephalic segment (see above). The basal joint of these is (except in *Scutigera*) fused with the sternal plate of the segment, and the anterior end of

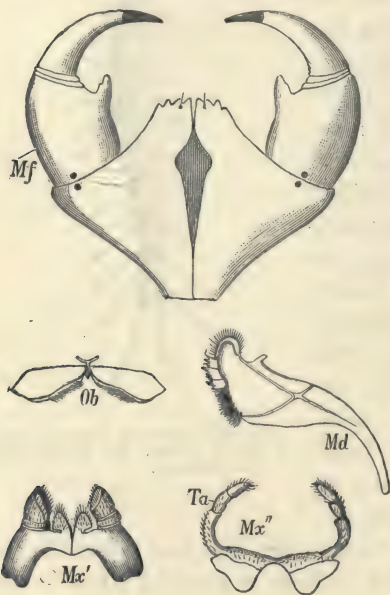


FIG. 358.—Mouth parts of *Scolopendra mutica* (after Stein). *Ob* Labrum; *Md* mandibles; *Mx'* first maxilla; *Mx''* 2nd maxilla; *Ta* palp; *Mf* maxillipeds (poison claws).

the plate so formed is often armed with teeth. The rest of the appendage consists of four segments, the femur, tibia, and two tarsalia; the distal tarsal is a sharp claw with the opening of the poison gland, which lies in the base of the appendage, at its apex. The tibia and proximal tarsal are, except in *Scutigera*, annular.

The body-segments frequently possess, in addition to the broad tergal and sternal plates, a number of small sclerites in the soft skin of the pleural region. In the Geophilidae (and to a less extent in the Scolopendridae) the tergal and sternal plates

of most of the segments are partially or completely divided into two, viz. an anterior pretergal plate and a pair of small presternal plates, but the segments never bear more than one pair of appendages each. The legs (see above), like the antennae, tend to vary in length inversely with the length of the body.

Normally they possess seven segments, a coxa, trochanter, femur, tibia, and three tarsalia the last of which ends in a claw. The legs of the last pair (anal legs) are attached to the antepenultimate (pregenital) segment and are usually longer than the preceding. The genital segment (*see above*) carries the median generative opening and usually a pair of genital appendages. The latter are better developed in the female, in which they are used in oviposition. They are absent in female Scolopendridae and in many male Lithobiidae. The anal segment is much smaller than the others and is without appendages.

Glands are found in the coxal joints of the last four or five pairs of legs (coxal glands); in the pleura of the last pedigerous segment; in the sternites of the segments (sternal glands) and in the anal segment (anal glands). The secretion of the sternal glands causes the phosphorescence found in some Geophilidae. The ventral pits are paired or unpaired pits found on certain of the sternal plates of some genera (some Geophilidae).

Of **sense organs**, besides the sensory hairs and spines of various forms found on the body generally and on the appendages, especially the antennae and jaws, may be mentioned the *maxillary organs* of *Scutigera*. These consist of a pit, richly lined by setae and supplied by a special nerve, on the inner side of each of the basal portions of the 1st maxillae. An organ of Tömösvary covered with hairs and similar to that of Diplopoda (p. 586) can very generally (apparently absent in Geophilidae) be made out. It is placed near the base of the antenna, and is supposed to be auditory in function. The eyes are simple ocelli, similar to those of Diplopods and Insects (p. 328). In *Lithobius* they are very closely aggregated. In *Scutigera* there are compound eyes, which are sometimes called pseudo-facetted eyes. They are, however, true compound eyes resembling in all essential points of structure those of Insects and Crustacea.

The **alimentary canal** consists of fore-gut or oesophagus (stomodaeum) lined by chitin; of mid-gut or enteron proper without chitinous lining; and of hind-gut or rectum (proctodaeum) which is lined by chitin and receives at its anterior end two long malpighian tubes. In the Scolopendridae and Geophilidae the oesophagus is of considerable length and the

rectum has an S-shaped curvature ; in *Lithobius* the oesophagus is short and the rectum is straight.

A number of glands, which may be called salivary, open in connexion with the mouth. In *Scolopendra* and *Scutigera* there are five pairs, in the Lithobiidae two or three pairs. The posterior of these open on the coxae of the first pair of legs and are coxal glands. In *Scolopendra* the two anterior pairs are contained in the head and open within the labrum into the buccal cavity. The two posterior pairs are much larger and extend from the 3rd to the 7th body-segment. Their ducts have a spiral fibre and open into the mouth in front of the 2nd maxillae.

The central **nervous system** consists of a bilobed cerebral ganglion (p. 328) in the head, supplying the antennae, the eyes, and organs of Tömösvary ; of a suboesophageal ganglion which supplies the jaws and the maxillipeds (the ganglion of the latter is distinct in the embryo), and of a ventral chain of ganglia, one of which occurs in each pedigerous segment. The ganglia of the first and second pedigerous segment are approximated. Behind the last there is a genital ganglion. The cerebral ganglion gives off a visceral nerve to the dorsal wall of the gut.

Vascular system.* The heart (Fig. 359), which is contained in the pericardium, extends nearly the whole length of the body from the first pedigerous segment backwards. It possesses a pair of ostia and gives off a pair of arteries in each segment, and in front it is continued as an artery to the cephalic organs. The arteries branch and finally end by opening into spaces in the connective tissue. Some of them terminate in small bodies resembling lymphatic glands (Kowalevsky's bodies). There is also a supraneural vessel lying along the dorsal side of the nerve cord and directly connected with the front end of the heart by a pair of arterial arches which embrace the gut. The perivisceral and pericardial cavities communicate by perforations in the pericardial membrane, and there are alary muscles in the floor of the pericardium. In spite of the peculiar local breathing organs of *Scutigera* the blood system in that animal is not essentially different from that of *Scolopendra*. The blood is colourless, but in *Lithobius* it is stated to have a slight violet tinge.

* G. Newport, *Phil. Trans.*, 1843. C. Herbst, *Bibl. Zool.* (Chun and Leuckart), Heft 9, 1901. O. Duboseq, *Arch. Zool. Exper.* (3), 6, 1897, p. 481.

The **fat-body** consists of aggregations of fat cells in the wall of the pericardial and perivisceral cavities. It appears to consist of a reticulum the cells of which contain fat, and is similar to the fat-body of *Onychophora*.

Except in *Scutigera* (p. 604), the **tracheae*** branch and anastomose, and possess a spiral fibre. They are distributed to the organs. The stigmata, which vary in number in the different forms, are placed on the pleural membranes (except in *Scutigera*), one pair in a segment. They are most numerous in the Geophilidae, in which all the pedigerous segments except the first and last possess a pair. They are never found on the head or on the segment of the poison claws. They may be slit-like (*Lithobius*, *Scolopendra*,

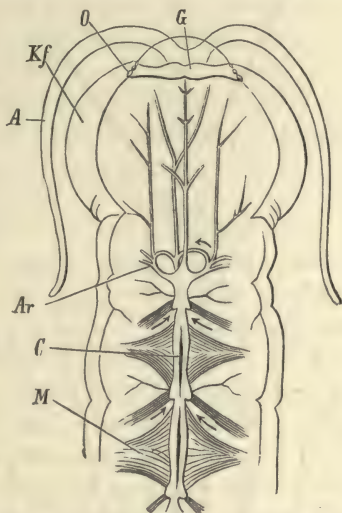


FIG. 359.—Head and anterior segments of *Scolopendra* (after Newport). *G* cerebral ganglion; *O* eyes; *A* antenna; *Kf* maxilliped (poison-claw); *C* heart; *M* alary muscle; *Ar* arteries.

etc.), funnel-shaped (Geophilidae), ear-shaped (*Otostigma*), or sieve-like (*Heterostigma*). The tracheal system of *Scutigera* is described at p. 604. In this form the stigmata are dorso-median, and the tracheae are without spiral fibre and practically unbranched.

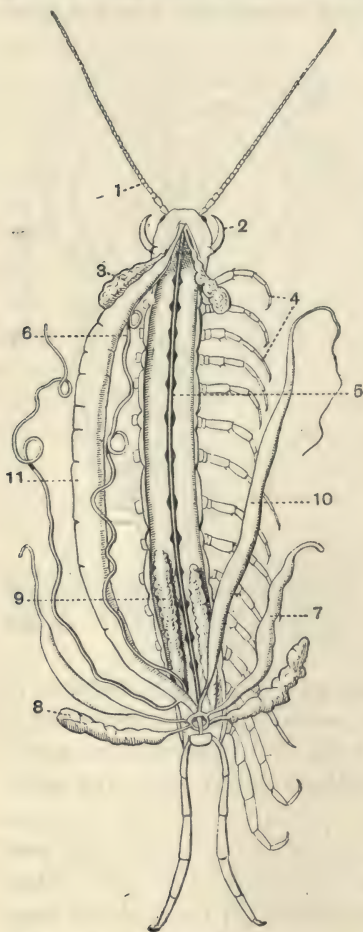
The **reproductive glands**† are placed in the middle and posterior portion of the body on the dorsal side of the gut. They open on the ventral surface immediately in front of the anus on the penultimate segment.

The ovary is single and median; it passes behind into an oviduct which divides into two. These embrace the rectum and join again beneath it to open by the median genital opening (*Lithobiidae*). In some forms one of these two oviducts is

* E. Haase, Das Respirationssystem der Symphylen und Chilopoda, *Schneider's Zoologische Beiträge*, 1, p. 65.

† B. Schaufler, Zur Kenntniss der Chilopoden, *Verh. Zool. bot. Gesel. Wien*, 1889, p. 465. C. Tönniges, Beitr. z. Spermatogenese u. Oogenese der Myriopoden, *Z.f.w.Z.*, 1902, 71, p. 328.

absent, or much reduced and functionless (*Geophilus*). A pair of receptacula seminis and two pairs of accessory glands are in connexion with the hind end of the oviduct.



From Shipley & McBride's *Zoology*.

FIG. 360.—*Lithobius fortificatus* dissected to show the internal organs (after Vogt and Jung). 1 Antenna; 2 poison-claw; 3 salivary gland; 4 walking leg; 5 ventral nerve cord; 6 malpighian tubule; 7 vesicula seminalis; 8 small accessory gland; 9 large accessory gland; 10 testis ending anteriorly in a filament; 11 alimentary canal.

The testis is more varied in form. In *Lithobius* (Fig. 360) it is tubular and median, and its duct divides behind embracing the gut and receiving two vesiculæ seminales; further back the two vasa deferentia unite and receive two pairs of accessory glands. In the Geophilidae there are two tubular testes, and in the Scolopendridæ several spindle-shaped testes which open into a median vas deferens; this divides behind, the duct of one side being reduced, to embrace the gut and pass to the external opening. In these cases the hind end of the vas deferens is coiled and there are two pairs of accessory glands.

Most Chilopods form spermatophores, but it is doubtful if copulation occurs. It has been stated that the males deposit spermatophores in places frequented by the females which then in some way take them up.

Development.* It has been stated that some of the Scolopendridæ are viviparous. However this may be, the majority

* Metschnikoff, *op. cit.* on p. 594. Heymons, *op. cit.* on p. 314. N. Sograff, On the embryonic development of *Geophilus* (Russian), *Nachricht Ges. Freunde Naturk. Anthr. u. Ethn. Moskau.*, 43, 1883. Korschelt and Heider, *op. cit.*

of Chilopods appear to be oviparous. *Lithobius* lays its eggs singly and rolls them in the earth. The European species of *Scolopendra* lay (in June and July) from 15 to 33 eggs (about 3 mm. in length) in the earth (3 to 8 cm. deep) and roll themselves round them, protecting them from contact with the earth and keeping them moist by a fluid secretion until they are hatched, which takes place after some weeks. *Geophilus* also has been observed to take care of its eggs in a similar manner. The egg is surrounded by chorion which is probably formed in the oviduct. The segmentation and formation of the layers appear to take place very much as in the Diplopoda. Mesoblastic bands are formed and become completely segmented into hollow somites. The number of these in the head has been already described (p. 320). In the body there is one pair of them for each pedigerous segment, and two pairs in the genital region behind the last pedigerous segment. The anal region (telson) and the acron are without them. Each somite (except the three anterior) becomes differentiated into three sections, a lateral in connexion with the appendage, a ventral over the rudiment of the future sternite, and a dorsal beneath the future tergite. The walls of these parts give rise to muscles, etc., and the cavities disappear except that of the dorsal section in some segments, in which it persists as the reproductive gland. The latter is therefore at first paired and segmented. So far as is known none of the somites give rise to a nephridial section.

The hypoblast surrounds the yolk, and gives rise to the walls of the intestine, the oesophagus and rectum being formed from ectoderm. The perivisceral spaces arise from the space between ectoderm and endoderm which becomes lined by mesoderm.

An embryonic cuticular membrane is formed by the ectoderm at an early stage, as in Diplopods, and is shed after hatching.

The postembryonic development of Chilopods takes place on two types. In Scutigleridae and Lithobiidae the young are hatched with seven pairs of legs, and the larval development consists in the formation of the remaining appendages as well as in the increase in number of ocelli and antennal joints and in the attainment of sexual maturity (so-called anamorphosis). In Scolopendridae and Geophilidae on the other hand the young are hatched with the full number of appendages (or of their rudiments), and the larval development consists of the complete

attainment of the adult form (epimorphosis). As in Diplopods the tracheae are in all cases not laid down until the larval period.

The Chilopods are active creatures which avoid light and prey upon other animals, though some of them may occasionally eat vegetable food. They bite their prey with the poison claws and kill it by the secretion of the poison-gland, which flows into the wound. Certain tropical species of large size are able to inflict wounds which are dangerous even to man.

Tribe 1. PLEUROSSTIGMA

With tracheal openings on the pleural area. The number of sterna never exceeds that of the terga.

Fam. 1. **Geophilidae**. With long, multisegmented vermiform body, short antennae of 14 segments, short legs, stigmata on all the postcephalic segments except the first and last. The number of segments usually variable in the same species. The labial palps are 3-jointed. The anal legs are short and eyes are absent. The sternal plates are usually perforated by pores of the sternal glands, the secretion of which causes the phosphorescence found in some species. They live in the surface soil or under stones, etc.; cosmopolitan. *Geophilus* Leach, *G. condylogaster* Latzel, Britain; *G. longicornis* Leach, Britain; *G. electricus* Mein., Britain. *Mecistocephalus* Newp. *Orphnaeus* Mein. *Himantarium* C. Koch. *Gonibregmatus* Newp. *Scolioplanes* Bergs. o. Mein. *Scotophilus* Mein. *Stigmatogaster* Latzel. *Orya* Mein. *Himantharium* Karsch.

Fam. 2. **Scolopendridae**.* With 21 or 23 leg-bearing segments; tergum of the basilar segment more or less completely fused with that of the first leg-bearing segment; antennae much shorter than the body, with 17 to 34 segments; ocelli either four on each side or absent; 9, 10, 11, or 19 pairs of stigmata present; palp of the 2nd maxilla with 3 joints and a claw; the anal legs are long and their basal segment fused with the pleural sclerite; agile forms, for the most part inhabiting warm countries. They leave the egg provided with the full number of legs. The bite of the large forms is dangerous to man. They live under stones, etc., or in holes, but emerge at night.

Sub-fam. 1. **Cryptopinae**. Without eyes (at most a clear spot on the edge of the head); tarsus unsegmented or indistinctly segmented; tibiae with one or two spurs or with the under side beset with bristles. Cosmopolitan. *Cryptops* Leach; *Theatops* Newp.; *Plutonium* Cav.; *Newportia* Gerv.

Sub-fam. 2. **Otostigminae**. With four eyes on each side; stigmata oval or round, placed obliquely to the long axis of body in anterior segments; tarsal spurs usually present; cephalic tergum never projecting over first postcephalic tergum. Australia, Asia, Africa, and warm parts of America. *Otostigmus* Por.; *Alipes* Imh.; *Rhysida* Wood.

Sub-fam. 3. **Scolopendrinae**. With four eyes on each side; stigmata triangular or slit-like, placed parallel to long axis of body; tarsal spurs absent or only one; cephalic tergum projecting back

* K. Kraepelin *Revision der Scolopendriden*, Hamburg, 1903.

over the first postcephalic tergum. Tropical and warmer temperate zones. *Pithopus* Poc. *Asanada* Mein. *Pseudocryptops* Poc. *Cupipes* Kohlr. *Colobopleurus* Kraep. *Cormocephalus* Newp. *Scolopendra* L. (Fig. 361).

Fam. 3. **Craterostigmidae**.* With 15 pairs of legs; with an intercalated tergite in front of the 3rd, 5th, 7th, 8th, 10th, and 12th and stigmata on the 3rd, 5th, 8th, 10th, and 12th pedigerous segments. The anus and genital openings are enclosed by a bivalvular sclerite. The sternite and pleura of the 14th pedigerous segment are completely fused, as are the sternum, pleura and tergite of the 15th. With one ocellus on each side. Tasmania. *Craterostigmus* Pocock.

Fam. 4. **Lithobiidae**. With 15 pedigerous segments, and tergites and sternites equal in number; tergites of the 2nd, 4th, 6th, 9th, 11th, and 13th pedigerous segments smaller than their neighbours; stigmata on the 3rd, 5th, 8th, 10th, 12th, and 14th pedigerous segments, and sometimes on the 1st; the tergite of the 1st segment not unusually large; anal and genital zones well marked off from one another, the latter in the male with more or less reduced, in the female with powerful, segmented and spurred generative processes. Anal legs longer than the others. Tarsal joints 3. Cosmopolitan.

Sub-fam. 1. **Cermatobiinae**. Body slender and fusiform; antennae flagelliform, shorter than body; eyes in one pair; palp of 2nd maxilla 3-jointed with claw; stigmata in 1st pedigerous segment. The minor tergites are deeply excavated behind and appear to be divided. Island of Adenara (Indo-Malaya). *Cermatobius* Haase.

Sub-fam. 2. **Lithobiinae**. Antennae fairly long but shorter than body, 13-100 joints; ocelli absent, or one pair, or numerous; palp of 2nd maxilla 3-jointed with claw; stigmata in 6 or 7 pairs. The minor tergites less excavated behind and do not appear double. *Lithobius* Leach (Fig. 357), many species, cosmopolitan. *Henicops* Newport, Tasmania, Australia, N. Zealand, N. America.

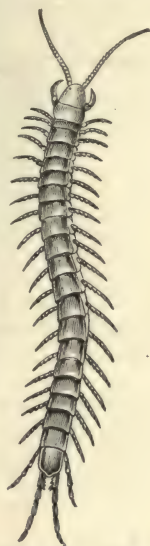


FIG. 361.—*Scolopendra morsitans* (from Claus).

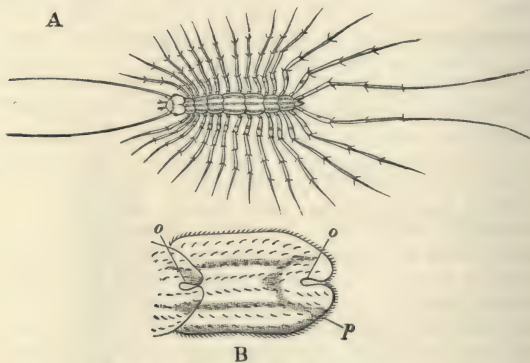
Tribe 2. NOTOSTIGMA

With tracheal openings in the dorsal middle line and with compound eyes. The number of sternites exceeds that of the tergites.

Fam. **Seutigeridae**. Body short and thick, with 15 pairs of legs (Fig. 362), long and increasing in length posteriorly. Antennae long, eyes compound (one pair), 1st maxillae with a sense organ beset with numerous rods, 2nd maxillae 5-jointed without claw and with spines on each segment except the terminal. The tergite of the poison claw segment visible but small. On the 15 pedigerous segments there are 8 distinct tergites, the tergites of segments 7-9 being fused and those of 2, 4, 6, 11, and 13 being very small and covered. The tracheal stigmata are 7 in number and

* R. I. Pocock, A new and annectant type of Chilopod, *Q.J.M.S.*, 45, 1902, p. 417.

placed in the dorsal middle line. They occur at the hinder edge of the 7 anterior of the 8 tergites above mentioned. They lead into tracheal



From the *Encyclopædia Britannica*.

FIG. 362.—A *Scutigera rubrolineata* (after Buffon). B Tergite and part of a second tergite of the same, enlarged to show the position of the stigmata o; p hinder margin of tergum.

warmer regions all over the world, under stones, etc., and especially in human dwellings. *Scutigera* Lamarek, *Sc. coleoptrata* L., Central and S. Europe.

Order SYMPHYLA.*

Small progoneate forms with 12 pairs of legs and a head possessing antennae, mandibles, maxillulae, maxillae and labium.

The Symphyla are small Myriapods, less than three mm. in length. They possess a distinct head, and a body which in being flattened dorso-ventrally recalls that of the Chilopoda. The body (Fig. 363) consists of 12 leg-bearing segments and of an apodal terminal segment, and of 12 apodal segments intercalated between these, so that there are 25 segments in all, behind the head. Sixteen (or fifteen) of these segments possess well marked dorsal scuta (Fig. 363), of which the first, which carries the first pair of legs, is the smallest. The legs are not grouped in pairs and there is no diplopody.

* Gervais P., Myriapodes, in Walckenaer, *Hist. Nat. des Insectes Aptères*, iv, Paris, 1847. Newport G., Monograph of the class Myriapoda, order Chilopoda, *Trans. Linnean Soc.*, 19, 1845, p. 373. Latzel R., *op. cit.*, 1884. Ryder J. A., Structure, affinities and species of Scolopendrella *Proc. Acad. Nat. Sci. Philadelphia*, 1881, p. 79. Grassi B., I progenitori degli Insetti e dei Myriapodi, *Morfologia delle Scolopendrelle*, *Mem. d. Reale Accad. d. Scienze d. Torino* (2), 37, 1886. Schmidt P., *op. cit.* Hansen H. J., The genera and species of the order Symphyla, *Q.J.M.S.*, 47, 1903, p. 1.

sacs from which tufts of tracheae (without spiral fibre) project into the pericardium and aerate its blood. The heart therefore receives arterial blood. Genital appendages are present in both sexes. The young when hatched do not possess the full complement of legs. They are very active animals. They are found in the

The head * carries a pair of long multi-articulate antennae and three pairs of jaws : these are one pair of 2-jointed mandibles ; a pair of maxillae bearing a short palp and ending in two lobes ; and a labium consisting of a median basal part carrying two pairs of small lobes. In addition there is a hypopharynx, on each

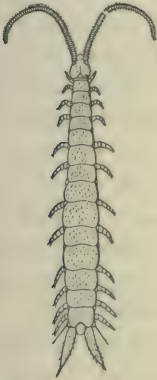


FIG. 363.—*Scutigera immaculata* (after Latzel).

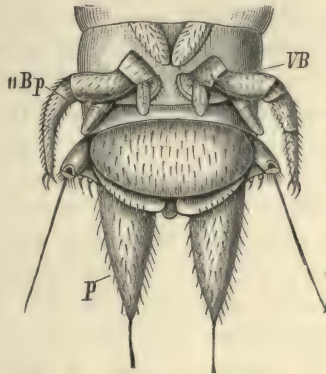


FIG. 364.—Ventral view of hind end of body of a young *Scutigera immaculata* (after Latzel). 11 Bp Eleventh leg; VB protrusible ventral sac; p cerci with spinning organ.

side of which is articulated a *maxillula* (Hansen, paraglossae of Grassi). The maxillulae probably represent the appendages of a segment, which is found in the embryo of some insects between the mandibles and 1st maxillae, and is supposed to be homologous with the segment of the 1st maxillae of Crustacea. Similar structures appear to be present in Collembola and Thysanura. In addition to these parts there is an upper lip. Eyes appear to be absent, or represented at most by a pair of ocelli. The legs of the first pair are placed on the segment following the head and are 4-jointed (in some species reduced to wart-like protuberances), the posterior eleven pairs being 5-jointed and ending in two claws. The legs of a pair are set tolerably far apart from one another (except those of the first pair). Close to the coxae (or on them, Schmidt) of the legs of the last ten pairs and on their inner sides there arise small movable processes called **parapodia** (Fig. 364) and just on the inner side of each of

* The constitution of the head of the Symphyla corresponds with that given in the column for Insects on p. 325.

these a protrusible sac (*V.B.*). The parapodia have been interpreted as the reduced posterior legs of a double segment and possibly serve as sense-organs. Haase suggests that the ventral sacs are homologous with the coxal glands of Chilopods and that they function as respiratory organs, being often associated with weak or absent tracheae. Attached to the end of the body is a pair of conical processes—the cerci—at the ends of which open the ducts of a spinning gland, the threads secreted by which may be used for attaching the eggs. They are regarded by Latzel as the appendages of the 24th body-segment. There is a pair of stigmata on the head beneath the insertion of the antennae. From each of these proceeds a strong tracheal trunk which is without a spiral thickening and undergoes a certain amount of branching but does not extend behind the third body-segment. The alimentary canal consists of pharynx, oesophagus, stomach, intestine and rectum. Two or four malpighian tubes open into the intestine, and the rectum has a chitinous lining. A pair of elongated salivary glands opens into the mouth. The fat-body is well developed and occupies the greater part of the body-cavity. There is a dorsal tubular heart provided with ostia, a cephalic aorta and a ventral vessel. The paired gonads are placed on each side of the gut and open to the exterior by a median opening on the ventral surface between the fourth pair of legs; in the male the two testes are connected by a transverse tube passing ventral to the gut. External sexual characters and genital appendages are absent. The nervous system consists of a supra-oesophageal ganglion and a ventral chain of ganglia. The adult stage is reached by a series of moults in which the segments and legs increase in number. The condition of the just-hatched form is however not known. The Symphyla are found in most parts of the world. They are active animals and appear to prey upon small insects. They avoid the light and are found under stones, etc., in damp places, and in moist mould at the roots of grass. They recall *Cam-podea* in their habits and appearance. The name Symphyla was given to the order by Ryder on the view that they combine insectan and myriapodan characters. They are myriapodan in the number of their legs and body segments, and in the position of the genital opening (Diplopoda); while of their insectan characters attention may be called to their biunguiculate legs

and to their jaws, which resemble those of insects in form and number, and to the presence of maxillulae, by which they approach the Thysanura.

Two genera, *Scolopendrella* Gervais, and *Scutigerella* Ryder, with about 24 species are known.

CHAPTER VIII.

CLASS IV. INSECTA.*

Arthropods having in the adult condition three pair of legs, usually two pair of wings and the body divided into three regions, (i) the head which bears a single pair of antennae and certain mouth parts, (ii) the thorax and (iii) the abdomen. Respiration tracheal. Young always more or less different from the adult and complete metamorphosis very frequent.

Insects are segmented animals and as in the Crustacea and the Arachnida the segments are grouped into higher categories. Three regions, or *tagmata* as Lankester calls them, the head, the thorax and the abdomen are present. The thorax always has three segments, but the number in the head and in the abdomen of an Insect body is still a disputed point. The two most dominant views are those of Heymons † and of Lankester, ‡ the latter of whom founds his enumerations on the researches of Folsom. § The discrepancy between these two views, which are fully discussed on pp. 318 ff., is readily seen from the following table :—

* D. Sharp, *The Cambridge Natural History, Insects*, London, vol. i, 1895, vol. ii, 1899. Berlese, *Gli Insetti*, now in course of publication, Milano. Packard, *Textbook of Entomology*, New York and London, 1898. Miall and Denny, *The Cockroach*, 1886. Henneguy, *Les Insectes*. Lowne, *Anatomy of the Blow-fly*. Lyonnet, *Traité anatomique de la Chenille qui ronge le bois de Saule*, The Hague, 1762. J. Lubbock, *On the Senses, Instincts and Intelligence of Animals with special reference to Insects*, *Int. Sci. Ser.*, lxxv, 1888, and *Tr. Linn. Soc.* London, xxiii, 1860. Newport, *Phil. Trans.*, 1837, p. 259. Kirby and Spence, *Introduction to Entomology*, London, v. Ed., 1828. L. O. Howard, *The Insect Book*, New York, 1901.

† Die Segmentirung des Insectenkörpers, *Abh. Ak. Berlin*, 1895.

‡ Article Arthropoda, *Encycl. Brit.*, 10th Ed., vol. xxv.

§ The Development of the Mouth Parts of *Anurida maritima* Guér, *Bull. Mus. Harvard*. xxxvi, 1900.

Heymons.*		Lankester and Folsom.	
"Acron."			
1 Segment (Pre-antennal) bears the eyes†		Eyes † (pre-antennal)	} Head
2 " bears Antennae	} Head	Antennae	
3 " disappears in embryo		Disappears in embryo	
4 " bears Mandibles		Mandibles	
5 " " 1st Maxillae	} Thorax	Superlingual Maxillulae	} Head
6 " " 2nd Maxillae		1st Maxillae	
7 " " 1st Thoracic legs		2nd Maxillae	
8 " " 2nd Thoracic legs		1st Thoracic legs	
9 " " 3rd Thoracic legs	} Thorax	2nd Thoracic legs	} Thorax
10 " = 1st Abdominal		3rd Thoracic legs	
11 " = 2nd Abdominal		1st Abdominal	
12 " = 3rd Abdominal	} Abdomen	2nd Abdominal	} Abdomen
13 " = 4th Abdominal		3rd Abdominal	
14 " = 5th Abdominal		4th Abdominal	
15 " = 6th Abdominal		5th Abdominal	
16 " = 7th Abdominal		6th Abdominal	
17 " = 8th Abdominal		7th Abdominal	
18 " = 9th Abdominal		8th Abdominal	
19 " = 10th Abdominal		9th Abdominal	
20 " = 11th Abdominal		10th Abdominal	
21 " = "Anal piece "		11th Abdominal	
"Telson"			

Heymons does not recognize the superlingual segment bearing the maxillulae, described by Folsom in the Apterygota. This segment is said to supply the dorsal element in the hypopharynx, a median structure or "tongue" which lies between the maxillae. He places the division between the head and thorax at the junction of the 6th and 7th segments, a position which corresponds with the division between the tagmata in the Crustacea. The Odonata, certain Orthoptera and the Dermaptera (earwigs), and Lepidopterous embryos show eleven abdominal segments, and, except in the Collembola, where the number is six, Insects have not less than ten abdominal segments.

It is interesting to note that both views assign twenty-one segments as the full complement for an Insect since this number has been asserted for the higher Crustacea and Arachnida.‡ In no Insect however can twenty-one segments be seen at one time. The appendages of the third disappear (*Campodea* is a probable

* *Zoologica*, 1901, p. 142. Heymons recognizes median anterior and posterior portions which he calls the "acron" and "telson" respectively; he calls the acron plus the pre-antennal segment the protocephalon.

† See also table on p. 325.

‡ In the lower Crustacea, and of course in the Myriapods the number of segments is greater, so that the significance of the identity of number in the higher forms is not apparent.

exception) during embryonic life. It corresponds with the second antennary segment of the Crustacea. In many cases, moreover, the abdomen does not form its full complement of segments, and, when it does, some of the hinder ones are pushed or telescoped into those in front and there is usually a certain suppression or atrophy of parts which tends to obscure the real number of segments.

The abdominal segments primitively bear paired appendages homologous with the legs, but these usually disappear. In the Collembola and Thysanura certain of these appendages persist and some authorities regard the processes which form the ovipositor in some Insects, as appendages and also the anal styles of the male cockroach. The cerci anales (cercopods) are with more certainty regarded as appendages.

The cuticle which covers all parts of the body of an insect embryo and which is infolded at the several apertures leading into the body, thickens in certain parts to form plates or sclerites. In a typical **segment** there are the following sclerites :—(i) the *tergum* or dorsal shield, each tergum consists originally of a right and a left half which unite in the middle line in the adult ; (ii) the *sternum* or ventral plate which may remain double. Between the terga and the sterna is usually a softer membrane, the *pleuron*, and in this may be found : (iii) an *epimeron* adjacent to the tergum, and (iv) an *episternum* next the sternum. In nature however all these four parts are seldom met with together, some may be suppressed, others greatly enlarged, so that the analysis of the exoskeleton of an insect's body, especially of the thorax, is a matter of no small difficulty.

The **head** of an Insect consists of a rounded chitinous case in which, except for the appendages, almost all traces of segmentation have disappeared. As a rule the following regions can be made out (Fig. 365). The *clypeus* is a somewhat flattened area between the bases of the two antennae extending ventrally to bear the *labrum*, which is a hinged flap overhanging the mouth. The labrum is sometimes lobed but is primitively a median process. The top of the head or *epicranium* runs from the dorsal limit of the clypeus—often marked by a suture—between the eyes on to the back of the head down as far as the neck. The region of the head surrounding the insertion of the neck is often referred to as the *occiput*,

and the hole left in the head, when it is cut off, as the *occipita foramen*. Running ventralwards behind the eyes from the epicranium to the base of the mandibles and on its inner surface giving origin to the stout mandibular muscle, is the *gena* or cheek. When the head is prolonged in an antero-posterior plane the region of the head between the occiput and the base of the fused second maxillae or *labium* is often distinct and is known as the *gula*.

Certain hard parts, strengthening the walls of the head and acting as surfaces for the origin of muscles, occur inside the head. As examples of these the *tentorium* of the Cockroach and the two hollow cylindrical pillars which pierce the head of the gnats may be cited.

There are two median processes, one in front, and one behind the mouth, which are known as the *epipharynx* and the *hypopharynx* respectively and which are not usually regarded as having the value of appendages. The former arises from the inner surface of the labrum and in most of the mandibulate insects exists as a membranous lining to that part and to the clypeus. It bears certain taste organs. In such piercing insects as the gnats and fleas it is prolonged with the labrum and helps to form the channel up which the blood of the prey flows. On the opposite or posterior wall of the mouth, lining the labium, is a median process which, when it remains soft and fleshy, is usually referred to as the *tongue* or *lingua* or *ligula*, but when as in gnats (Fig. 376) it is prolonged and forms a projecting process, it is termed the *hypopharynx*. On it the salivary ducts open. The hairy grooved organ of bees, which projects from the middle of the labium, is usually called the *ligula*: there is much uncertainty about its homologies.

According to Heymons the first segment of the head forms the clypeus and labrum, whilst the epicranium and genae are formed from the tergites, or elements of the tergum, of the three jaw-bearing segments whose fused sternites form the hypopharynx.

The head is united with the thorax by a short flexible *neck* whose wall is often strengthened by certain chitinous thickenings called the *cervical sclerites*.

The **thorax** is composed of three segments, the *pro-*, *meso-* and *meta-thorax*. These remain fairly distinct in such insects as the

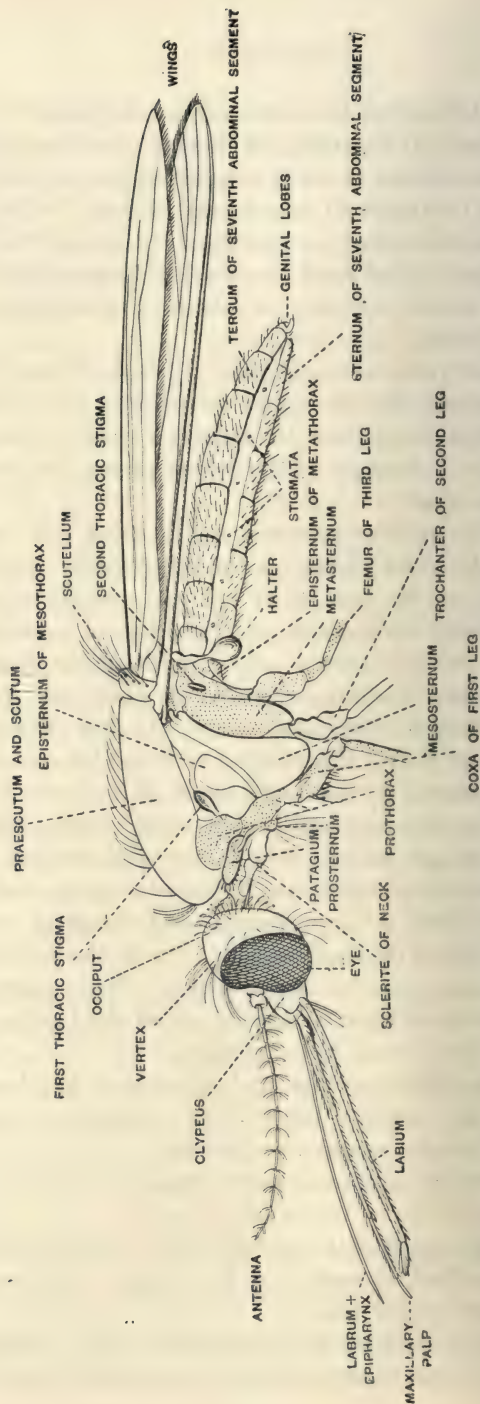


FIG. 365.—Side view of a female *Anopheles maculipennis* Meigen \times about 22 to show the various parts of the body. The prothorax and meta-thorax with their respective legs are dotted (from Nuttall and Shipley).

running Orthoptera, but in insects whose flight is powerful they are closely fused together and it is difficult to analyse the thorax into its component parts (Fig. 335). In such insects the terga of the meso- and meta-thorax, or *mesonotum* and *metanotum* as they are called, may each be divided into as many as four areas called the *praescutum*, *scutum*, *scutellum* and *postscutellum* respectively. The pleuron in each of the three segments is usually divided into an *episternum* and an *epimeron*; and to these with the sterna the three pairs of legs are attached. A pair of lobes or sausage-shaped projections, termed *patagia*, lie on each side of the prothorax in Diptera and Lepidoptera. They give origin to the attachment of certain muscles in the Culicidae. A somewhat similar pair of processes, the *tegulae*, on the meso-thorax overlying the base of the fore-wings in Lepidoptera and certain Hymenoptera are sometimes, but probably on

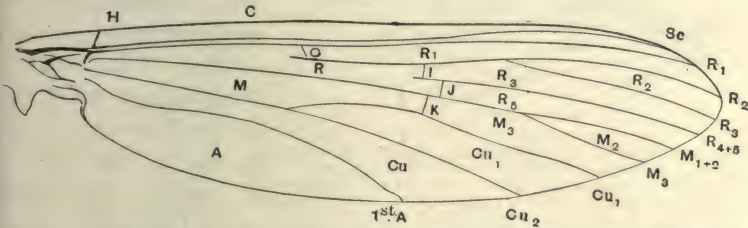


FIG. 336.—The right wing of a male *Anopheles maculipennis* Meigen \times about 14 (from Nuttall and Shipley). The scales have been removed to show the nervuration. The nervures and cells are named after the plan of Comstock and Needham. A anal area; 1st A anal nervure; C costa; Cu cubitus; H humeral cross-nervure; I cross-nervure between R_2 and R_4+5 ; J cross-nervure between radial and medial systems; K cross-nervure between medial and cubital systems; M media; O cross-nervure between R_1 and R_2 ; R radius. Sc subcosta.

insufficient grounds, homologized with the wings. In the higher members of the latter group the first abdominal segment becomes, in the imago, so fused with the thorax as to seem to belong to this region. A curiously complicated skeleton of *apodemes* or processes for the attachment of muscles is often present in the thorax; it varies much in different insects.

The **wings** are confined to the meso- and meta-thorax and in the great majority of cases both pairs are present. If one pair only exists it is almost always the meso-thoracic and in one large class the Diptera the meta-thoracic wings are replaced by the so-called *halteres** or balancers. Many of the more primitive

* οἱ ἀλτηρες = dumb-bells used in jumping.

Insects are wingless and in most groups there are certain species that have lost their wings. In some cases this apterous condition is found only in one sex and in many species there is a correlation between the simple eyes or *ocelli* and the presence of wings. Both structures tend to disappear simultaneously.

The attachment of the wing to the thorax lies along the lateral edge of the tergum and is often of a very complex nature. When the wing is expanded it is seen to be roughly triangular in shape, the apex being at the point of attachment. The anterior edge in this position is called the *costa* (Fig. 366 *C*), the external is called the *outer margin* and the posterior is called the *inner margin*.

The wings are outgrowths of the skin, which consists in its

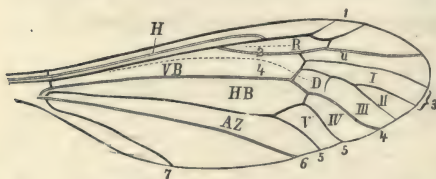


FIG. 367.—Wing of *Tipula* (after Fr. Brauer). *H* subcosta; *1* first longitudinal nervure (*costa mediana*); *2* radial rib (*radius* or *sector*); *3* cubital rib; *4* discoidal rib (or *cubitus anticus*); *5* submedian (or *cubitus posticus*); *6* anal rib (or *postcosta*); *7* axillar rib; *R* marginal cell; *U* submarginal cell; *D* discoidal cell; *I-V* posterior marginal cells; *VB* anterior basal cell; *HB* posterior basal cell; *AZ* anal cell.

simplest condition of a layer of hypodermal cells covered by a thin secretion, the cuticle. The outgrowths may arise in the embryo or larva in one of two ways: (i) either the skin grows out and “the wings begin—and always remain—as ex-

ternal folds or evaginations,” or (ii) the wings commence by an ingrowth into the body, which eventually, either by turning inside out or by some other means, becomes external. At least 90 per cent. of existing insects belong to the latter category which form the **ENDOPTERYGOTA**. Those whose wings are external throughout life form the group **EXOPTERYGOTA**.

The membranous expansions which form the tissue of the wings are strengthened and supported by the *nervures* as an umbrella is spread on its ribs (Fig. 367). The arrangement of the nervures is of the greatest systematic importance. The areas they bound are termed *cells*. The nervure primitively consists of a channel in which blood circulates, and this channel is usually traversed by a trachea and by a rod-like bar known as “Semper’s rib.”

The hard, thickened fore-wings of the **Coleoptera** are termed

elytra. In them the chitinous cuticle is much thickened and the upper and lower surfaces are clamped together by minute chitinous pillars. Between these layers, fat-bodies and cells containing uric-acid concretions, as well as nerves, tracheae and blood are found.

The fore-wings of the Strepsiptera are replaced by small

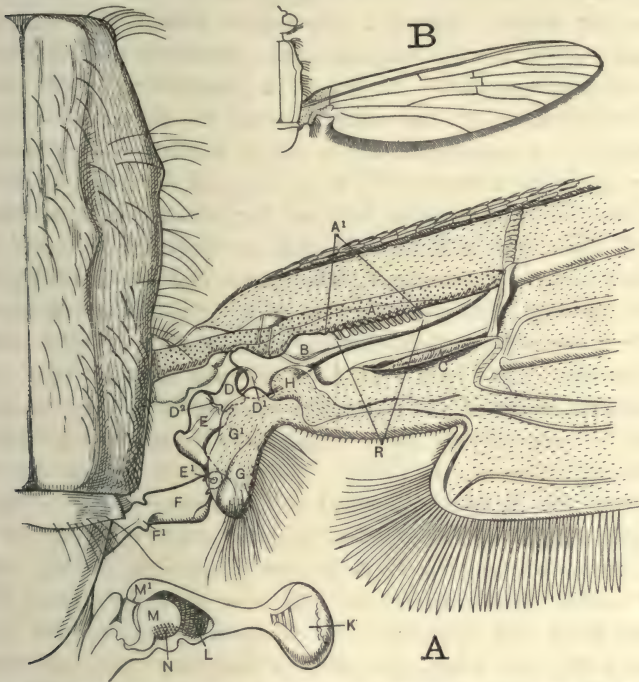


FIG. 338.—A, right half of thorax of *Anopheles maculipennis* with base of right wing and right halter. Magnified 40 times. B, the same magnified about 7 to show the area which bears the stridulator. This is shaded. R toothed bar; A¹ the teeth which rasp on the ridges borne by B; B blade bearing the ridges R; C trough which limits the movements of B; D distal chitinous sclerite bearing a claw which works in D¹ the hollow at the base of B; D² joint between D and E; E intermediate sclerite between D and F; E¹ hinge between E and F; F proximal sclerite which is inserted into the thorax beneath the scutellum; F¹ process on F; G thickened edge of squama; G¹ fold of squama overhanging E and D; H process of chitin which overhangs the base of the blade; K distal end of halter; L concave area covered with papillae; M knob; M¹ hinge; N papillae on knob (from Shipley and Wilson).

membranous appendages. In the Diptera the hind-wings are replaced by the above mentioned *halteres*, which are usually clubbed and well provided with sense-organs. In most of the more primitive orders the fore- and hind-wings are quite unconnected and move independently, but in many

Lepidoptera they are loosely linked together by a structure termed the *frenulum* and *retinaculum*, whilst in the Hymenoptera they are closely knit together by a row of hooks on the anterior edge of the hind-wing which play over a ridge on the posterior rim of the fore-wing.

The rapid vibration of the wings of insects, which in the house-fly attains the number of 335 beats a second and in the bee 440 beats per second, makes a perceptible noise. The humming or buzzing which is so characteristic a feature of the Diptera and Hymenoptera seems to be due to a fundamental note caused by the vibration of the wing through the air and to certain overtones. A mechanism which would produce such overtones has recently been described * at the base of the wings in certain Diptera. It consists of a toothed bar which works against a ridged blade and it is thought that as the wing is raised and lowered these two structures grate against one another (Fig. 368).

No one now holds the view that the wings are homologous with the true appendages, † though their real nature is still a matter of dispute. The view was formerly put forward that they are modifications of the plate-like tracheal gills such as those borne on very varying parts of the body by the larval Sialidae, Perlidae, Odonata, etc., etc. They certainly resemble the tracheal gills in being supplied with tracheae and with blood, but the details of the tracheal system differ markedly in the two structures, and the view is now abandoned. It is moreover evident that whereas the gills arise at very varying parts of the body and appear to be temporary adaptations to an aquatic life, the wings arise always from the meso- and meta-nota. Thus Fritz Müller's ‡ view that wings are modifications of lateral outgrowths of the dorsal surface of these segments and not of any larval organ has much to commend it.

The third division of the body or **abdomen** is not so inelastic and compacted together as are the head and thorax. It is capable of considerable extension, a necessary consequence of its containing the larger part of the alimentary canal and the ovary,

* On a possible Stridulating Organ in the Mosquito (*Anopheles maculipennis* Meig.) by A. E. Shipley and E. Wilson, *Tr. Roy. Soc. Edin.*, xl. 1902, p. 367.

† A typical segment bears a pair of appendages usually directed ventrally, such appendages form the gnathites and the legs, and are referred to here as true appendages.

‡ *Jena'sche Zeitschr. Naturwiss.*, ix, 1875, p. 241.

organs which vary greatly in size under certain conditions and at different times. Hence the sclerites are separated from one another by soft areas and frequently overlap one another (Fig. 369). There is as a rule a *tergum* or *notum* and a *sternum* united together by a soft pleural membrane, the *pleuron*, which typically bears a *stigma*, or external opening of the tracheal system. A pleural sclerite is sometimes present. The first abdominal segment is often modified and in many Hymenoptera it seems to

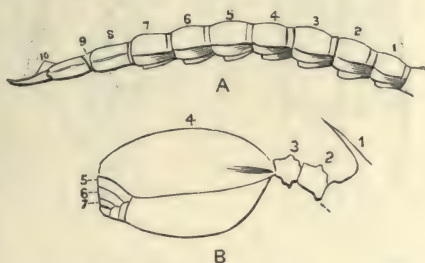


FIG. 369.—Simple abdomen of *Jappa*. (A) contrasted with the highly modified one of an ant, *Cryptocerus* (B). The abdominal segments are numbered from before backwards. (From Sharp.)

have passed over into the thorax (Fig. 369 B). At the posterior region also great modifications and often reductions of parts occur; usually one or more of the hinder segments are invaginated into their predecessors and become modified in connexion with oviposition and copulation. The number of abdominal segments visible in an insect is therefore usually smaller than the number which really exists. According to Heymons twelve segments are found in cockroach and earwig larvae and the same number in much later stages of some dragon-flies; the twelfth segment giving rise to the "anal-piece." This seems to be the maximum number; ten segments are perhaps the commonest number, but there may be—and usually appear to be—fewer. Heymons does not recognize the serial homology of the first and last segments (acron and telson) of the body with those between, and therefore he does not consider the supra-anal and sub-anal laminae which when present lie above and below the anus as terga or sterna. The podical plates of the Cockroach are probably developments of the sub-anal sclerite.

The **appendages** (v. note p. 616) are processes borne by the segments, typically one pair by each segment, though in the adult those of the abdominal segments are usually absent. They are as a rule jointed and contain muscles, nerves, tracheae, and blood.

The appendages of the pre-antennal segment are absent in

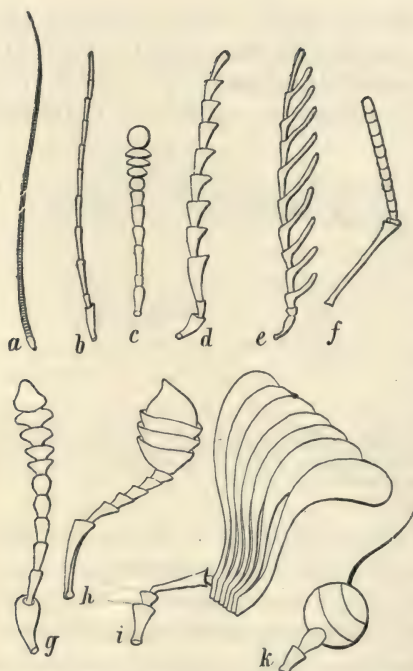


FIG. 370.—Different forms of antennae (after Burmeister). *a* Bristle-like antenna of *Locusta*; *b* filiform antenna of *Carabus*; *c* moniliform antenna of *Tenebrio*; *d* dentate of *Elater*; *e* pectinate antenna of *Ctenicera*; *f* crooked antenna of *Apis*; *g* club-shaped of *Silpha*; *h* knobbed of *Necrophorus*; *i* lamellated of *Melolontha*; *k* antenna with bristle from *Sargus*.

the adult unless the eyes represent them.* These will be dealt with under the organs of sense.

The appendages of the *second* segment are the antennae. These are usually long, multi-segmented processes, but they may be reduced to a few segments, or even to one. They vary very greatly in structure and are of much use in classification (Fig. 370). They often exhibit sexual differences. They are obviously of the greatest importance to the insect and act as sense organs, partly tactile, partly olfactory and partly auditory in nature.

The appendages of the *third* segment—if we

accept the view, as there is very good reason to do, that an intercalary segment exists between that which bears the antennae and that which bears the mandible—disappear in the adult except in the primitive family Campodeidae† where they persist as paired tubercles.

The appendages of the *fourth* segment are the mandibles. These never bear a palp as they do in most Crustacea (Fig. 371). They may be toothed, stout, unjointed ‡ structures as in biting insects, or they may be modified into sickle-shaped or even tubular piercers as in the larvae of some water beetles, or they may take the form of piercing, slender blades as in Hemi-

* *v.* tables on p. 325 and on p. 609, and the discussion on p. 349.

† H. Uzel, *Zool. Anz.*, xx, 1897. W. M. Wheeler, *J. Morph.*, viii, 1893, p. 1.

‡ Traces of segments are described in the mandibles of some beetles.

ptera and most Diptera. In some may-flies and caddis-flies and Diptera, and in the Macrolepidoptera they quite disappear in the adult stage.

The appendages of the *fifth* segment are, according to Heymons, the 1st maxillae, and according to Folsom the maxillulae.

According to recent workers* a complete and separate pair of gnathites succeed the mandibles in the Apterygota (Collembola and Thysanura) which have been variously termed *paraglossae*, *superlinguae* and *maxillulae* (Fig. 372). These maxillulae are reduced to the merest vestiges in the winged Insects (Pterygota).

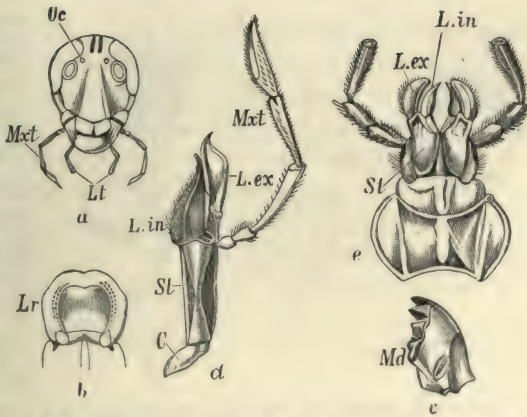


FIG. 371.—Mouth parts of a *Blatta* (after Savigny). *a* Head seen from the front; *Oc* ocelli; *Mxt* maxillary palp. *Lt* labial palp; *b* upper lip (labrum, *Lr.*); *c* mandible (*Md*); *d* 1st maxilla; *C* cardo; *St* stipes; *L.in* lacinia; *L.ex* galea; *e* 2nd maxillae or labium (lower lip), clearly composed of two halves.



FIG. 372.—Right maxillula of *Machilis maritima* $\times 72$ (after Carpenter). 1 lacinia; 2 galea; 3 palp.

The first maxillae in the least specialized cases consist of a segmented base (protopodite) composed of two pieces, the proximal called the *cardo* and the distal called the *stipes*. The *stipes* ends in two lobes, the inner called the *lacinia*, the outer the *galea* (Fig. 371). At the junction of these with the *stipes* is inserted on the outer edge, the segmented palp, obviously a sensory and tactile organ. Any of these parts may be much modified; thus in the *Lepidoptera*, the *galea* is elongated and grooved and so united with its fellow as to form a tube, through which the liquid food is sucked, the *lacinia* and palp

* H. J. Hansen, *Zool. Anz.*, xvi. 1893, pp. 193 and 201. J. W. Folsom, *Bull. Mus. Comp. Zool.*, Harvard, xxxvi, 1900, p. 87. G. H. Carpenter, *P. Irish Ac.*, Ser. B, xxiv, 1903, p. 325.

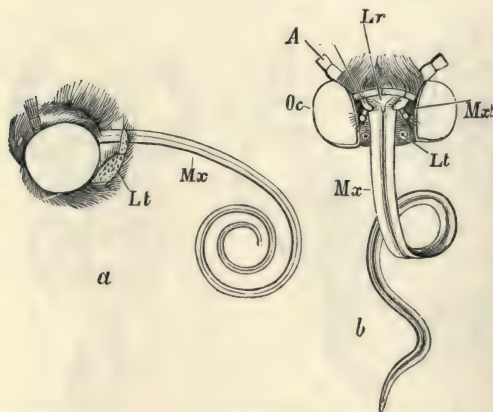


FIG. 373.—Oral apparatus of Butterflies (after Savigny). *a* of *Zygaena*; *b* of *Noctua*. *A* antennae; *Oc* eyes; *Lr* upper lip; *Mxt* maxillary palp; *Mx* maxilla (first); *Lt* labial palp, cut away (in fig. *b*).

being deficient. On the other hand in the *Hymenoptera* the lacinia is enlarged to form a piercing blade whilst the galea and palps are reduced (Fig. 374). In Hemiptera (Fig. 375) and many Diptera the 1st maxillae become piercing stylets; in the former group the palps are absent

but they are conspicuous in many flies (Fig. 376).

The sixth segment, or seventh, according to Folsom, bears the 2nd maxillae with parts similar to the 1st maxillae, but the cardines are usually fused to form a median piece the *sub-mentum*, the two stipes are more or less fused and form

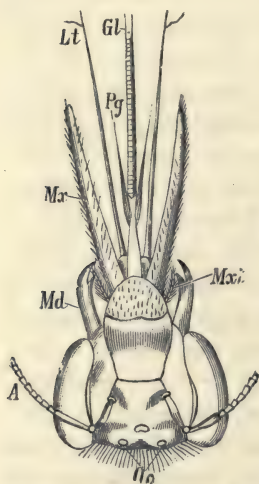


FIG. 374.—Mouth parts of *Anthophora retusa* (after Newport). *A* Antennae; *Oc* ocelli; *Md* mandibles; *Mx* maxillae; *Mxt* maxillary palp; *Lt* labial palp; *Gl* ligula; *Pg* paraglossae.

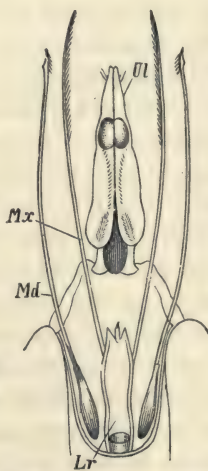


FIG. 375.—Mouth parts of *Nepa cinerea* (after Savigny). *Ul* Lower lip (labium) or rostrum; *Lr* upper lip; *Md* mandible; *Mx* maxilla (first).

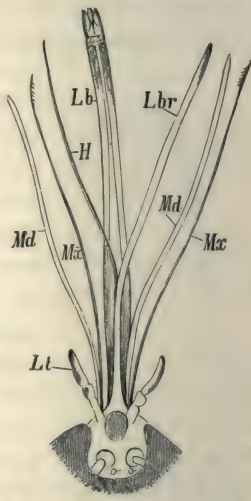


FIG. 376.—Mouth parts of *Culex memorosus* (after Becher). *Lbr* upper lip; *Lb* lower lip (proboscis); *Lt* labial palp; *Md* mandibles; *Mx* maxillae (first); *H* hypopharynx (piercing weapon).

the *mentum*, while the part corresponding with the galea of the 1st maxillae is often termed the *paraglossa*, median to which, when it exists, is the *lacinia*. Each second maxilla normally bears a palp. The complex formed by the fused second maxillae is often termed the *labium* or lower lip (Fig. 375). All the parts may undergo profound modification. The Hemiptera have their labia modified to form a jointed sheath in which the stylet-like mandibles and 1st maxillae lie, the labial palps are reduced (Fig. 375). In the Diptera the labium is also said to form a grooved proboscis and the palps persist. In many Hymenoptera the mentum is drawn out into a long narrow structure (Fig. 374).

The mandibles, and the first and second maxillae are often referred to as the mouth-parts or *trophi*. The homologies of these parts in the several Orders is a matter of some divergence of opinion and the whole subject would well repay a thorough revision based on embryological research.

The *seventh*, *eighth* and *ninth* (eighth, ninth and tenth according to Folsom) segments always take part in the formation of the thorax and, in the case of the Hymenoptera, the first abdominal is pushed forward and included in this tagma. The appendages of the first three are legs, and these three pairs of legs, confined in the imago to the three typical thoracic segments, are very characteristic of Insects. The legs are usually described as consisting of the following segments (i) the *coxa*, a



FIG. 377.—Different form of legs (règne animal). *a* *Mantis* with predatory leg; *b* leg of *Carabus* used in running; *c* of *Acridium* used in springing; *d* of *Gryllotalpa* used in digging; *e* swimming-leg of *Dytiscus*.

stout piece sometimes fused with the side or under surface of the thorax; (ii) the *trochanter*, a minute, often triangular segment; (iii) the *femur*; (iv) the *tibia*; (v) the *tarsus*; this may in rare cases be absent, it may also consist of but one segment but more usually it consists of any number of segments up to five which is perhaps the commonest number (Fig. 377). The

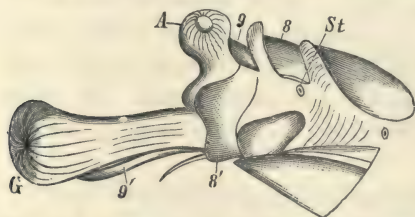


FIG. 378.—Posterior end of body of a Beetle (*Pterostichus* ♂) (after Stein). 8, 9 dorsal plates; 8', 9' ventral plates; St stigma; A anus; G genital opening.

tarsus ends in two claws (rarely in one) between which very frequently a lobe, the *empodium* or, when hairy, the *pulvillus*, projects. This may, e.g. in the Diptera and Hymenoptera, attain a great complexity of structure.

The legs of insects may undergo great modifications. They may become broad and thick for digging, broad and flat for swimming (Fig. 377), they may develop a comb for cleaning the antennae, or hairs for collecting pollen, or auditory organs as in the case of the Locustidae (Fig. 394) and Gryllidae, or stridulating organs as in the Acridiidae. Very rarely are legs absent in the imago stage.

The remaining segments belonging to the abdomen as a rule bear no appendages. There are however exceptions, the larvae of the Lepidoptera and of the saw-flies are provided with a varying number of feet in this region of the body. These differ in structure from the thoracic limbs and are termed *prolegs*. Again the members of the Order Thysanura bear in the adult a greater or smaller number of projections, one pair to each segment, which are usually looked upon as homologous with appendages, and some em-

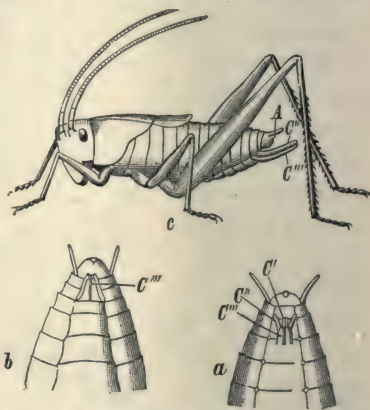


FIG. 379.—a Hind end of abdomen of a young female *Locusta* with the protuberances of the ovipositor and the anal styles; C' and C'' the internal and external protuberances of the penultimate; C''' the same of the antepenultimate segment. b slightly older stage. c nymph; A anus with anal styles (after Dewitz).

bryo Insects exhibit similar structures. Finally there are certain structures borne at the hinder end of the abdomen which are regarded by some, though there is no general agreement on this point, as of the nature of limbs. Amongst these are (i) the *cercopods* or *cerci anales*, usually segmented processes, tactile in function, which both in their appearance and their use resemble antennae; (ii) the three, paired elements of the *ovipositor*, which is developed in the females of certain Thysanura, Orthoptera, Odonata, Hemiptera, Physapoda and Hymenoptera, in which last named order the ovipositor is often modified to form a saw or a sting. It is formed, generally speaking, from processes of the seventh, eighth and ninth abdominal segments, though in many cases it appears that the posterior two pair of processes arise together from the ninth (Fig. 379); (iii) certain *claspers* and other processes connected with the male intromittent organ and with copulation which seem to have an origin similar to that of the component parts of the ovipositor with whose claim to be regarded as true appendages theirs must stand or fall.

The Alimentary Canal. Embryologically the alimentary canal is divided into (a) the *stomodaeum* or *fore-gut* which gives rise to (i) the mouth and pharynx, (ii) the oesophagus (Fig. 380), (iii) the crop, (iv) the proventriculus or gizzard; (b) the *mesen-*

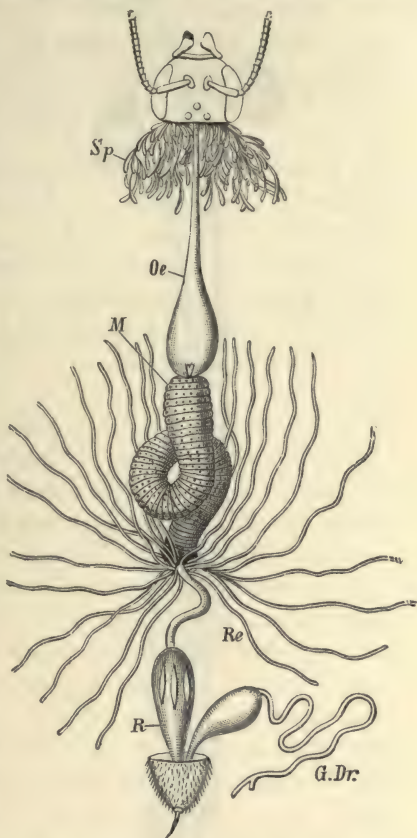


FIG. 380.—Digestive apparatus of *Apis mellifica* (after Léon Dufour). *Sp* salivary glands; *Oe* oesophagus with crop-like dilatation; *M* chylific ventricle; *Re* malpighian vessels; *R* rectum with so-called rectal glands; *G. Dr* poison glands!

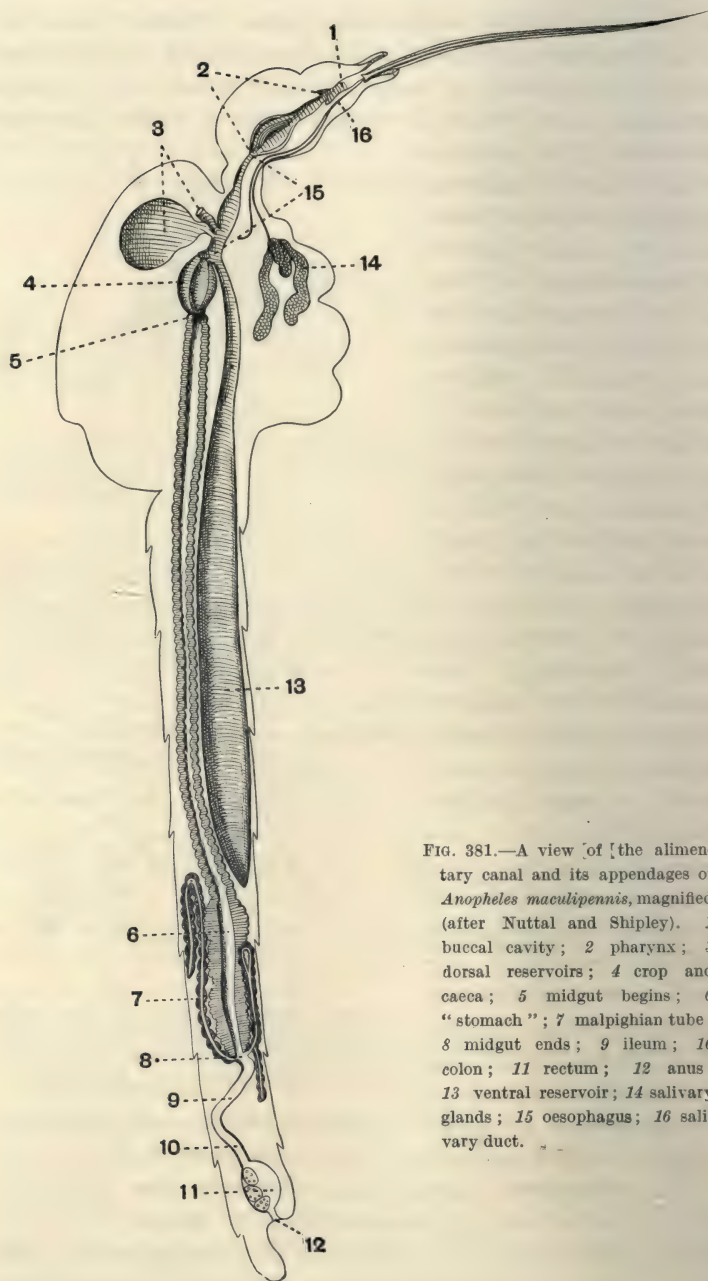


FIG. 381.—A view of [the alimentary canal and its appendages of *Anopheles maculipennis*, magnified (after Nuttall and Shipley). 1 buccal cavity; 2 pharynx; 3 dorsal reservoir; 4 crop and caeca; 5 midgut begins; 6 "stomach"; 7 malpighian tube; 8 midgut ends; 9 ileum; 10 colon; 11 rectum; 12 anus; 13 ventral reservoir; 14 salivary glands; 15 oesophagus; 16 salivary duct.

teron or *mid-gut* which alone is lined by endoderm and is usually small, in some cases it is even absent; it forms (v) the chylific ventricle which usually is provided with certain caecal glands; (c) the *proctodaeum* or *hind-gut* which is divided into (vi) the ileum which bears the malpighian tubules, (vii) the colon and (viii) the rectum and anus. The epiblastic stomodaeum and proctodaeum usually retain their chitinous lining throughout life. In many insects one or more of the eight parts mentioned above cannot be recognized.

In many larvae the alimentary canal is no longer than the body and is consequently straight, but in most imagoes it is longer and the excess in length has to be accommodated by coiling it into one or more loops, a rather rare feature in Arthropods. Again in the larvae of many Hymenoptera, some Coleoptera and Diptera and a few others the partition between the mid-gut and hind-gut persists and the larva is physiologically apterous until a late period.

The *mouth* leads into a *pharynx* which in those insects that suck fluid food has chitinous walls. Normally the walls enclose a triradiate lumen, but by the contraction of numerous muscles which run from the outside of the pharynx to the inside of the skeleton of the head this lumen can be enlarged until in section it is almost circular and the fluid food then rushes into it (Fig. 381). The *oesophagus* is a simple tube running from the pharynx to the crop. It traverses the neck and enlarges into the *crop* which has muscular walls. In certain insects which take liquid food one or more food-reservoirs open into the end of the oesophagus. These are present in the Diptera (Fig. 381, 13), Lepidoptera and Hymenoptera and they are usually but erroneously called "sucking stomachs"; they take indeed no part in the imbibition of the food, which is simply stored therein, until it is wanted elsewhere. A good deal of the digestion goes on in the crop when present. The saliva of many Insects, which is alkaline, converts the starch there into glucose which passes through the walls into the blood. The acid secretion of the caecal glands of the chylific ventricle is passed forward and assists in the emulsifying of fats and the conversion of albuminoids into peptones. The *proventriculus* is well developed in many Orthoptera and Coleoptera and many ants. The oesophagus is in some species produced into it, like a funnel in a tumbler,

and thus forms a valve (Fig. 382). The proventriculus is very muscular and often bears inside chitinous teeth and bristles which act as an efficient strainer. In the bees it forms the so-called "honey-stomach." The *mid-gut* or *chylic ventricle* is the only part of the alimentary canal not lined by chitin; it forms a simple tube but gives off a certain number of glandular caeca. The *intestine*, which is developed from the proctodaeum, bears anteriorly

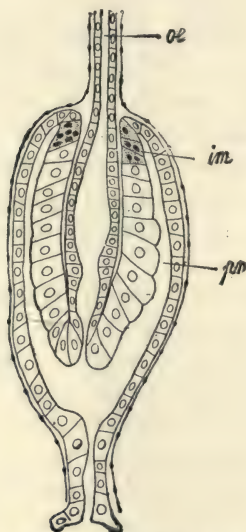


FIG. 382.—Longitudinal section through the larval proventriculus of one of the *Muscidae* (after Kowalevsky). *im* stomodaeal imaginal ring; *oe* oesophagus; *pn* proventriculus.

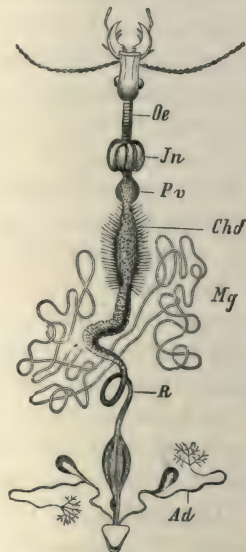


FIG. 383.—Alimentary canal and glandular appendages of a Beetle (*Carabus*) (after L. Dufour). *Oe* oesophagus; *Jn* crop; *Pv* proventriculus; *Chd* chylic ventricle; *Mg* malpighian tubes; *R* rectum; *Ad* anal glands with vesicle.

the malpighian tubules. It may or may not be divided, chiefly by variations in its diameter, into an *ileum* and a *colon*, and ends in a usually enlarged *rectum*. This often bears on its inner surface a certain number of papillae composed of a few large cells richly supplied with tracheae. It is possible these papillae are respiratory, a possibility strengthened by the fact that the larvae of dragon-flies breathe largely by anal respiration.

A curious cuticular tube is found in many adult insects and their larvae apparently secreted by the cells lining the chylic ventricle and parts of the intestine; it is termed the "peritrophic

membrane" and it prevents all contact of the food with the walls of the alimentary canal.

The glands which open into the intestine are (i) the salivary glands which normally open into the stomodaeum and secrete a fluid used in digestion. There are generally a pair on each side of the oesophagus, but there may be as many as eight pairs in the bee and often a reservoir as well. Their united ducts open on the hypopharynx. In the case of certain blood-sucking insects, e.g. mosquitoes, the fluid is conveyed down the hypopharynx into the tissues of the animal bitten and it is of a somewhat poisonous nature. Unless some of it be sucked up again with the blood it can take no part in digestion. The irritation is said to be caused by the excretions of certain yeast-cells which are found in the reservoirs. (ii) The silk-glands of certain larvae e.g. the silkworm, also open on that part of the labium called the lingua or hypopharynx; it is tempting to regard them as salivary glands; they are said to entirely disappear during pupation. (iii) The caecal glands of the mid-gut are usually two, six or eight in number or very numerous and scattered over the anterior end of this region of the gut. Their acid secretions act somewhat as does the pancreatic fluid of the Vertebrata. (iv) The malpighian tubes are the chief organs for nitrogenous excretion.

Excretory organs. The malpighian tubules are caecal extensions of the hind-gut and they usually open into its anterior end, but in the Psyllidae they are said to have shifted forward to the mid-gut whilst in certain Hemiptera they open into the

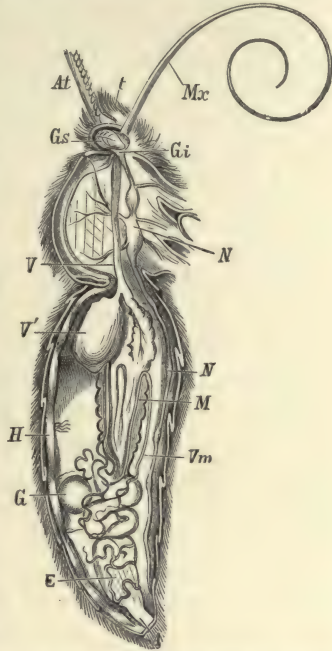


FIG. 384.—Longitudinal section through the body of *Sphinx ligustri* (after Newport). *Mx* maxillae forming the proboscis; *t* palp; *At* antenna; *Gs* brain; *Gi* subesophageal ganglion; *N* thoracic and abdominal ganglia; *V* oesophagus; *V'* suctorial stomach; *M* mesenteron; *Vm* malpighian tubes; *H* heart; *G* testes; *E* rectum; *A* anus.

rectum. They are wanting in Collembola and aphids. They vary greatly in number from two to a hundred and fifty and an attempt has been made to use their number in the classification of the Insecta.*

These tubules, as is often the case in glandular structures, are lined by very large cells with very large nuclei, they contain uric acid and urates of soda and of ammonia and also crystals of leucin and taurin. These substances are passed out of the body by the intestine. The products of nitrogenous excretion are also found in certain cells known as pericardial cells, which are found in and about the pericardium, and in the fat-bodies. It is said—but it is very doubtful—that the fat-bodies store away the urates throughout life (cf. Tunicata) and that the pericardial cells give theirs up to the blood which transmits them to the malpighian tubules.

The Circulatory System. The body-cavity of an Insect is not coelomic but haemo-coelic. It is full of blood and all the organs of the interior are floating in blood. The blood is usually colourless, but is greenish in those insects which feed on leaves; sometimes it is yellowish or brownish, and in the "blood-worm," the larva of the Dipteron *Chironomus*, it is coloured red with haemoglobin. The blood contains leucocytes which arise from certain cellular masses, which differ in position in different insects and closely resemble the fat-bodies.

The blood is moved about by a pulsating heart, which underlies the dorsal exoskeleton of the abdomen in the median line and is contained in a pericardium. It consists of a series, usually eight in number, of pyramidal chambers, in whose walls are circular muscle-fibres. The apex of each chamber opens into the base of the chamber just in front and so forms a funnel. On each side of the base of each chamber is an opening or *ostium* through which the blood enters the heart and is then driven forward. Arriving at the anterior chamber it passes into a non-contractile aorta which traverses the thorax and in the neighbourhood of the brain discharges the blood by an opening into the general body-cavity again. There is also a ventral channel which lies on the nerve-cord and is faintly contractile. It drives the blood from before backward.

Separating the pericardium from the body-cavity is a perfor-

* Brauer, *SB. Ak. Wien.*, xci, 1885, p. 237.

ated membrane, attached to which are paired *alary muscles*; whose outer ends are inserted into the under side of the terga. The contraction of these enlarges the pericardial space around the heart and the blood passes through the perforations of the pericardium toward the ostia. The exact function of the pericardial membrane and its muscles is still a matter of dispute.

There are certain structures found in the body-cavity of insects which play a part in the nutrition and excretory processes of these animals. These are (i) the **Fat-bodies**. This term is applied to masses of opaque, white cells crowded with minute fat globules and often with urates. They arise from the mesoblast and are often metamerically arranged. The fat-bodies evidently play a part in the general metabolism of the insect and from their smaller size in the imago than in the larva of some species it would seem that they act as a food supply during pupation. (ii) The **Pericardial Cells**. These occur around the heart and on the pericardial membrane and are sometimes metamerically arranged. They also are said to contain urates, and some authorities attribute to them a phagocytic action. (iii) The **Phosphorescent Organs**. These are most usually found in the beetles; in the abdomen in *Lampyris* and in the thorax in *Pyrophorus*. Essentially they are plate-like modifications of the fat-body shining through the body wall and like the fat-body are richly provided with tracheae. Their light is the most economically produced we know, since no energy is wasted by the production of heat, and all the radiation lies between the two ends of the visible spectrum. In those cases which have been investigated, the spectrum of the phosphorescent light gives no dark bands but is perfectly continuous. The usual view of the function of these organs is that they serve to attract the other sex. Emery * however holds that they act as a danger signal, a warning sign that their possessor is inedible. (iv) The **Oenocyte cells**. These are clusters of very large cells, the largest in the body except the ova, they are found usually in the abdomen of winged insects attached to the end of tufts of tracheae. Unlike the fat-bodies mentioned above, they arise from the ectoderm, being pushed in with the tracheae, and are segmentally arranged. Although they somewhat resemble the blood corpuscles they are

* *Zeitschr. wiss. Zool.*, xl, 1884, p. 338, and *Bull. Soc. ent. Ital.*, xvii, 1885, p. 351.

not believed to give rise to them, and their exact function is by no means settled.

The Respiratory System.

Insects breathe by means of tracheae or branching, elastic tubes, which as a rule communicate with the atmosphere by means of pores called *stigmata* or *spiracles* at their outer ends, and at their inner are distributed to all the fixed cells in the body. Since each cell has a direct air-supply the respiratory function of the blood is reduced to a minimum.

The tracheae from the fact that they contain air appear of a silvery brightness. Each

FIG. 385.—Tracheal branch with finer twigs (after Leydig). *Z* cellular external wall; *Sp* cuticular lining (spiral fibre).

consists of a chitinous lining continuous with the chitinous exoskeleton; this is secreted by a single layer of well-marked cells continuous with the epidermis. The chitinous layer is

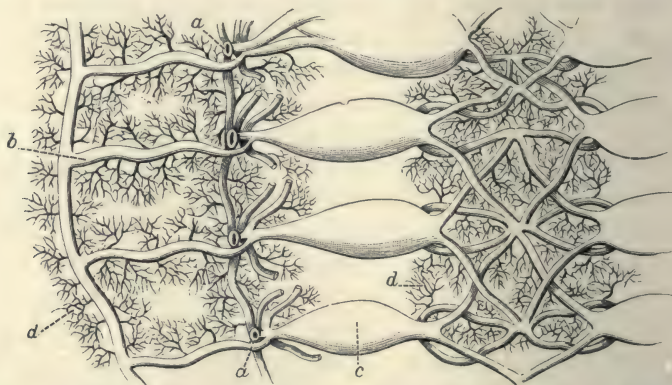


FIG. 386.—Portion of the abdominal part of tracheal system of a Locust (*Oedipoda*). *a* spiracular orifices; *b* tracheal tubes; *c* vesicular dilatations; *d* tracheal twigs or capillaries (after L. Dufour).

strengthened by spiral threads sometimes called *taenidae* which project on its inner surface and serve to prevent the tube from collapsing. In insects which fly actively the tracheae in

some cases expand to form large air vesicles. In these swellings the spiral strengthening is missing, as well as in the terminal capillaries of the tracheae.

The *stigmata*, by means of which the air enters and leaves the tracheae, are arranged as a rule along the sides of the thorax

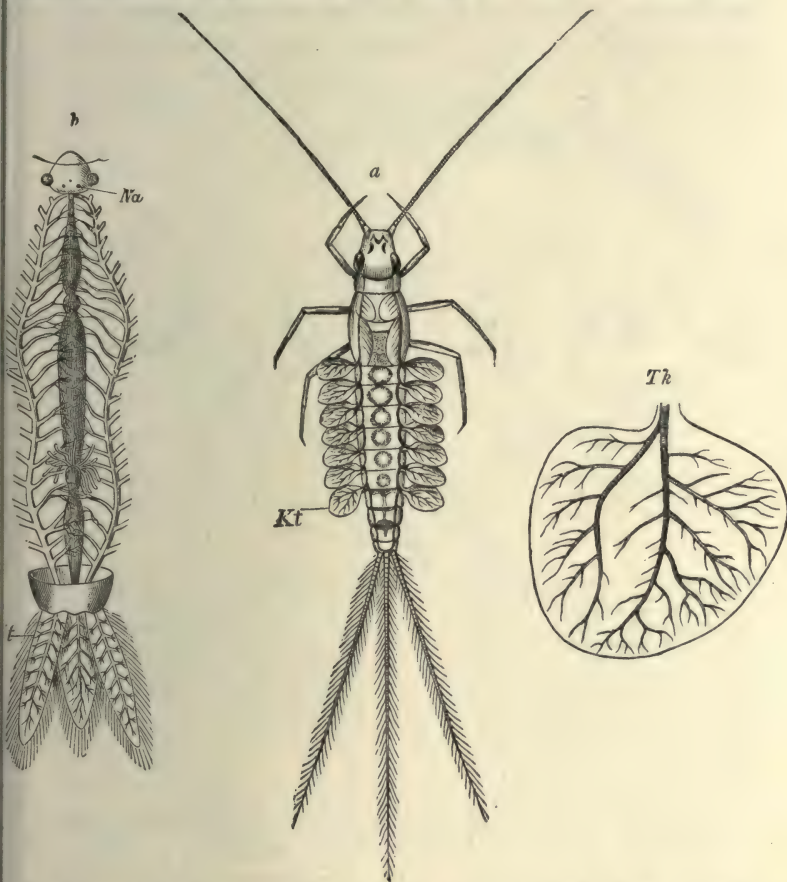


FIG. 387.—*a* Larva of *Ephemera* with seven pairs of tracheal gills *Kt*, slightly magnified. *Tt* an isolated tracheal gill, strongly magnified; *b* tracheal system of an *Agrion* larva (after L. Dufour); *Tst* tracheal trunk; *Na* accessory eyes.

and abdomen. They are oval slits with often a complicated armature which may bear bristles or hairs to keep out the dust. In many forms the opening can be closed. As a rule the stigmata lie in the pleura or soft tissue between the terga and sterna, usually two pairs on the thorax and ten on the abdomen, but the

number and position are subject to great variations. The air to a slight degree doubtless enters by diffusion, but insects also exhibit very marked respiratory movements; the abdomen contracts and expands many times a minute and these muscular movements doubtless assist the passage of the air up and down the tracheae. Except in certain Thysanura the tracheal system associated with one pair of stigmata communicates with all the others by means of longitudinal passages (Fig. 386). Thus if by accident one stigma be blocked, the parts supplied through it receive air from the neighbouring stigmata.

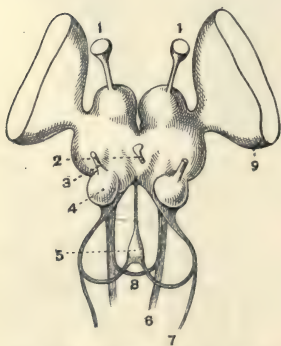


FIG. 388.—Dorsal view of the brain of *Melanoplus femur-rubrum* magnified (after E. Burgess). 1 ocelli; 2 median ocellar nerve; 3 antenna nerve; 4 antenna or olfactory lobe; 5 ganglion of sympathetic nerve; 6 oesophageal commissure to sub-oesophageal ganglia; 7 nerve to labrum; 8 cross nerve or commissure between the brain and sub-oesophageal ganglia; 9 optic ganglia.

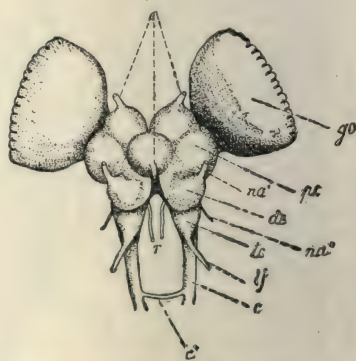


FIG. 389.—Anterior (ventral) aspect of the developed brain of *Oedipoda* (after Viallanes). c circum-oesophageal commissure; c' transverse commissure behind the oesophagus; dc deutocerebrum; go optic ganglion; lf labro-frontal nerve; na' accessory antennal nerve; no nerves of the three ocelli; pc protocerebrum; r root of the paired stomato-gastric ganglion; tc tritocerebrum.

In the larvae of many aquatic and certain parasitic insects the tracheal system is closed and this secondary condition is termed *apneustic* as opposed to the normal state of affairs known as *holopneustic*. The respiration then takes place through the thin integument of the body or through special tubular or leaf-like gills, which are richly supplied with tracheae and present a large surface to the oxygen-containing water. This general respiration is supplemented in the Odonata larvae by a marked anal respiration. When tracheae are present in aquatic larvae they are often much modified in position and their stigmata may

be borne at the end of elongate processes of the body as in *Eristalis* and in the Culicidae. Water-insects in the imago state have open stigmata and they come to the surface to breathe. They usually have some arrangement which enables them to entangle beneath their elytra or elsewhere some bubbles of air which they carry beneath the surface and use during their lengthy submergence.

The Nervous System. The central nervous system of an insect consists of a brain, an infraoesophageal ganglion and a chain of paired ventral ganglia extending through the thorax and abdomen. Typically there is one pair of ganglia to a segment, but they tend to undergo a considerable amount of fusion and suppression even in the abdomen.

Embryologically the brain* consists of three fused pairs of ganglia (Fig. 389), (i) the *procerebrum* † which forms the optic lobes and supplies the eyes; (ii) the *deutocerebrum* which is regarded as primitively postoral but which has become preoral

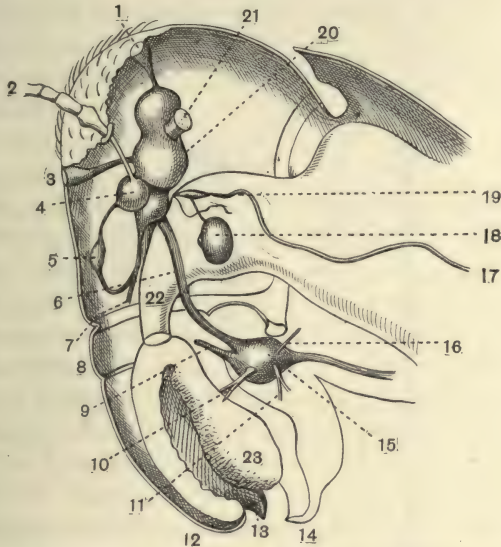


FIG. 390.—Side view of the head of *Melanoplus femur-rubrum*, the left wall of which has been removed to expose the brain (after E. Burgess). 1 ocelli and nerves leading to them from the two hemispheres; 2 antenna; 3 median ocellar nerve; 4 antennal or olfactory lobe; 5 frontal ganglion of sympathetic nerve; 6 oesophageal commissure to suboesophageal ganglion; 7 nerve to labrum; 8 clypeus; 9 nerve to mandible; 10 maxillary nerve; 11 labial nerve; 12 labrum; 13 mandible; 14 labium; 15 suboesophageal ganglion; 16 unknown nerve; 17 stomatogastric or sympathetic nerve; 18 posterior sympathetic ganglion; 19 anterior sympathetic ganglion; 20 optic lobe sending off the optic nerve; 21 optic nerve; 22 beginning of oesophagus; 23 base of first maxillae.

* See also pp. 320 and 321.

† The procerebrum of insects is according to Heymons (*Zoologica*, xiii, Heft. 33, 1901. "Die Entwicklungsgeschichte der Scolopender," p. 143) the homologue of the protocerebrum *sensu stricto*, together with the syncerebrum of Myriapoda.

by the shifting backwards of the mouth ; this supplies the antennae ; (iii) the *tritocerebrum* which theoretically supplies the lost intercalary or premandibular segment and which sends branches to the labrum (Fig. 389). This part of the brain probably takes a large share in the formation of the circumoesophageal commissures which end in the infraoesophageal ganglion. This, like the supra-oesophageal nerve-mass, is composed of three fused pairs of ganglia, which correspond with the mandibular and

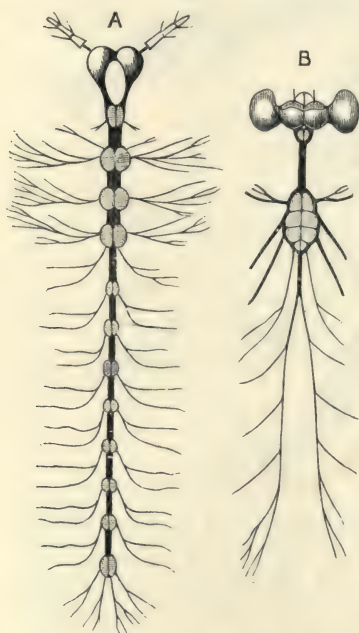


FIG. 391.—Cephalic and ventral chain of ganglia. A larva of *Chironomus* ; B imago of *Hippobosca* (after Brandt).

1st and 2nd maxillary segments respectively. The infraoesophageal ganglion supplies these appendages and contains a maxillula neuromere (Fig. 390). It also sends nerves to the salivary glands. In some genera, e.g. *Nepa*, *Acanthia* and a few others, the infraoesophageal ganglion is fused with the first thoracic, but the more usual arrangement is that this ganglion is followed by a series of three others which belong respectively to the pro- meso- and meta-thorax, and supply nerves to the appendages, muscles and other structures in these regions. The nervous system has typically a pair of ganglia for each abdominal segment, but a greater or less

fusion nearly always takes place. The posterior ganglion is always complex, and the entire abdominal chain may be concentrated into one ganglion, as in *Gyrinus* and in many Diptera (Fig. 391 B), or even drawn up into the thorax and fused with the meso- and meta-thoracic ganglia as in *Lachnosterna fusca*. This concentration reaches its height in the parasitic Diptera Pupipara where infraoesophageal, thoracic and abdominal ganglia are fused into one common mass.

A system of "sympathetic" or "stomatogastric" nerves

with associated ganglia arises from the tritocerebrum and supplies the labrum and alimentary canal. It is partly median in position.

Sense Organs. (i) The eyes of insects are of two kinds, compound and simple.

The *compound* eyes are sometimes regarded as homologous with a pair of appendages borne on the most anterior segment of the head. They consist of a number of ommatidia (v. p. 329), sometimes many thousand, and may occupy a very large area of the surface of the head. They

may as in the case of the blind termites and in many cave-insects be altogether suppressed. In the Diptera and Hymenoptera and others, in which the eyes reach a high degree of perfection, there is a distinct portion of the brain, the optic tract, from which the optic nerves originate. The *simple* eyes are usually two or three in number, but may be as many as twenty, grouped on each side of the head. They are entirely wanting in the Dermaptera and in certain Hemiptera and some other insects, and to some extent their presence is correlated with a well-developed power of flight.

(ii) The *olfactory* organs of insects appear to reside in the antennae, and their terminal structures take the form of minute hairs partially sunk in microscopic pits. These exist in



FIG. 393.—Head, thorax and abdomen of an *Acridium* seen from the side. *St* stigmata; *T* tympanic organ.

extraordinary numbers; for instance each antenna of the male cockchafer is said to be provided with some forty thousand of these organs.

(iii) The *auditory* organs. In comparatively few insects are there well developed, specialized auditory organs. Certain

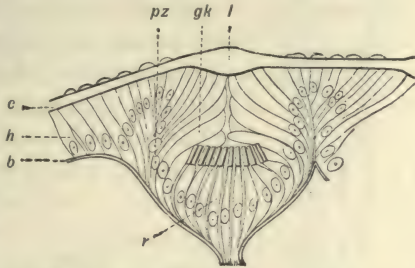


FIG. 392.—Section through the eye of a Coleopterous larva (*Dytiscus*) (after Grenacher, from Hatschek's *Text-book*). *c* chitinous cuticle; *l* corneal lens; *h* hypodermis; *pz* pigment-cells; *gk* vitreous body; *r* retina; *b* basal membrane.

hairs scattered over the body, and in some of the Diptera the hairs on the antennae, are sensitive to sound. Such hairs are

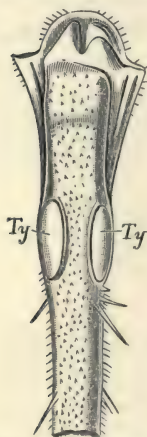


FIG. 394.—Tibia of the anterior leg of *Locusta viridissima* (after V. Graber). *Ty* tympanic membrane with operculum

termed *chordotonal organs*. The numerous, delicate hairs on the antennae of the male Culi-
cidae are set in vibration by the humming of the female and their heads are readily turned in the direction of the female when she begins to buzz. The basal joint of the antennae forms a socket richly supplied with sense organs and containing a large ganglion. The inclination of the antennae lodged in this socket doubtless conveys much information to the gnat. In the Acridiidae a more specialized organ is found on the anterior segment of the abdomen. This is provided with a drum or tympanum surrounded by a chitinous ring. On the inner face of the tympanum are a couple of horn-like processes to which a vesicle full of fluid is attached. This vesicle is said to act like the membranous labyrinth; it is in connexion with the auditory nerve which arises from the third

thoracic ganglion. Somewhat similar structures are found on the tibiae of the Locustidae, Gryllidae and Termitidae (Fig. 394).

(iv) *Organs of taste and touch*. Insects undoubtedly have marked preferences, but it is difficult for us to distinguish between their organs of taste, smell and touch. Certain hairs on the epipharynx and other parts of the mouth are probably organs of taste, whilst others on the palps may subserve the functions both of taste and touch. The body of an Insect being encased in a hard unyielding exoskeleton is mainly dependent on certain hairs (well supplied with nerves (Fig. 395) which project from almost all parts of the body) for the knowledge it gains of the outer world by touch.

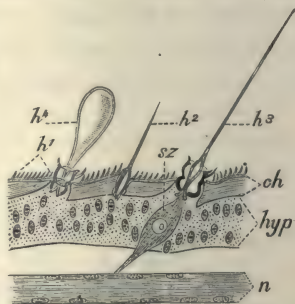


FIG 395.—Longitudinal section of portion of caudal appendage of *Acheta domestica* (after Vom Rath). *ch* chitin; *hyp* hypodermis; *n* nerve; *h*¹ integumental hairs, not sensitive; *h*² ordinary hair; *h*³ sensory hair; *h*⁴ bladder-like hair; *sz* sense-cell.

It being impossible to become an insect, it is also impossible to know what an insect feels and appreciates. It is more than probable that insects have sense organs which have no counterparts amongst vertebrate animals and these we cannot even hope to investigate. It is further practically certain that the range of eyes, ears and other sense-organs differs from that of the corresponding sense-organs in man. Insects probably hear sounds we cannot hear and see things hidden from our eyes, but the difficulty of research in this direction is great and at present we are in a state of very considerable ignorance as to their powers of sensation.

Reproductive Organs. Insects are bisexual, but occasionally parthenogenetic. Both ovaries and testes are confined to the abdomen and as a rule to the posterior part of it. In a few cases, as in the Thysanura, the ovarian tubules are segmentally arranged though united by a common oviduct on each side, and stretch throughout the abdomen. In the great majority of cases the external orifice is situate between the eighth and ninth segments, but it may be one segment in front, or one segment behind this level.

The organs are paired and as a rule there are several ovarian tubules; in the queen termite some fifteen hundred, in the queen bee some hundred, but usually six or eight occur on each side of the body (Fig. 396). Within these the ova are formed and the tubules on each side unite into an oviduct. Primitively the right and left oviduct opened independently, a condition of things which still obtains in the Ephemeridae and in *Lepisma*, but in other insects the two oviducts unite into a common,

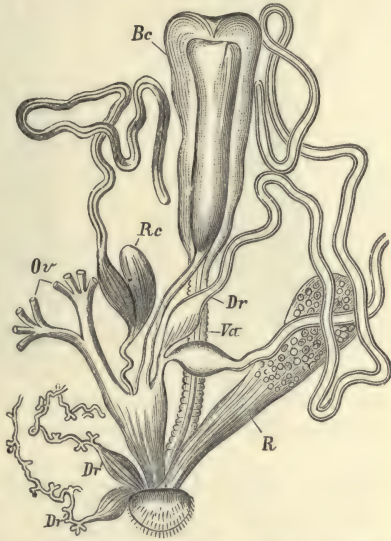


FIG. 396.—Female sexual organs of *Vanessa urticae* (after Stein). *Ov* the ovarian tubes cut off; *Rc* receptaculum seminis and accessory glands; *Va* vagina; *Bc* bursa copulatrix with duct leading to the oviduct; *Dr* glandular appendage; *Dr'* glandulae sebaceae; *R* rectum.

muscular vagina which opens to the exterior. At the anterior end of each ovarian tubule the cells are undifferentiated. As they approach the exterior they fall into groups (Fig. 397). In the simplest case as in the Cockroach (i) where there are no nutritive cells, the eggs lie in a row one behind another and each egg is surrounded by a layer of minute cells, which secrete the chorion or thick outer cover of the egg which is pierced by

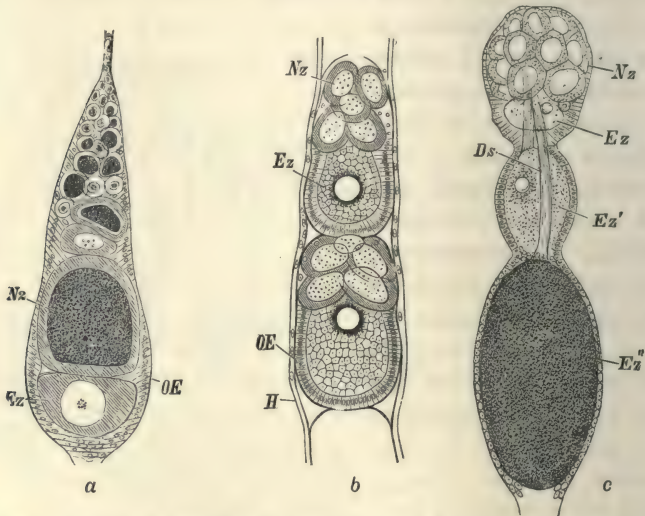


FIG. 397.—*a* egg tube of *Forficula*. *Nz* nutritive cells; *Ez* ovum; *OE* epithelium of the wall of the egg tube. *b* median part of the egg tube of a moth. *Nz* nutritive cells of the yolk-chamber; *Ez* ovum in the germ-chamber; *H* connective tissue investment, so-called serosa. *c* egg-tube of *Aphis platanoides* with three ovarian chambers (*Ez-Ez''*) and the terminal nutritive chamber with its cells *Nz*; *Ds* yolk cord.

a micropyle for the entrance of the spermatozoon. A more usual arrangement is (ii) where, between two consecutive egg-cells, there lies a mass of nutritive cells which are gradually absorbed as the egg approaches the vagina. This is found for example in *Dytiscus*. A third condition (iii) is that in *Rhizotrogus* where the ends of the ducts are swollen and form a nutritive chamber in which the eggs absorb food as they pass through it.

Certain accessory glands usually open into the vagina and secrete such structures as the "cocoon" which surrounds the batches of eggs of the cockroach. A spermatheca is also often found and has as a rule an opening distinct from that of the vagina. In the case of bees the spermatozoa retain their

vitality in the spermatheca of the queen-bee for over a year. The ova are fertilized internally, and are laid singly or in clusters, or in a cocoon (ootheca) as in the cockroach.

The testes are less conspicuous than the ovaries. Each may consist of a long tubular gland, but more usually they are tufted and provided with a number of follicles. In many Orthoptera, Coleoptera, Lepidoptera and Hymenoptera the right and left glands may be closely united and appear as one. Each opens into a vas deferens, which may be short or long. At the outer end each vas deferens usually swells to form a vesicula seminalis in which the spermatozoa accumulate; they then unite into an ejaculatory duct which is protrusible. As in the corresponding parts of the female the ducts of the male usually bear certain accessory glands of often doubtful function, though in some species they supply a secretion which forms the packets containing the spermatozoa (spermatophores). The spermatozoa of insects, unlike those

of most Arthropods, are provided with vibratile flagella.

Development. In the course of their life many insects undergo profound changes in their constitution and in their form. The egg as a rule gives rise to a *larva* which forms the predominantly feeding and assimilating stage. The larva is succeeded by a *pupa* or *chrysalis* stage, a period of quiescence during which many

of the tissues are disintegrated and rebuilt. This in turn gives rise to the *imago*, during whose life as a rule little growth occurs, but the animal is given over almost entirely to reproduction. A few insects produce their young already freed from the egg-

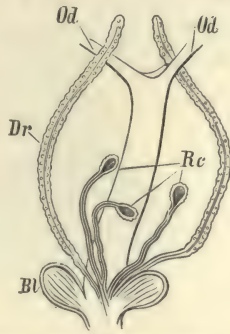


FIG. 398.—Terminal region of the female generative organs of *Musca domestica* (after Stein). *Od* oviduct; *Rc* the three receptacula seminis; *Dr* glandular appendages of the vagina; *Bl* blind sac-like appendage.

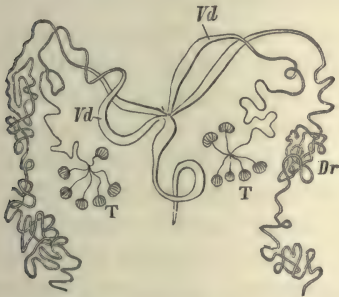


FIG. 399.—Male generative organs of the Cockchafer (after Gegenbaur). *T* testes; *Vd* dilated portion of the seminal duct; *Dr* coiled accessory gland.

shell and are then said to be viviparous e.g. some Muscidae, a few Oestridae, and the Pupipara amongst the Diptera, the Strepsiptera, the Aphidae and certain Ephemoptera. All others lay eggs, that is, are oviparous.

Occasionally the egg develops parthenogenetically *i.e.*, without fertilization. This takes place in the Aphidae, where parthenogenesis

is limited to a few generations, and in the Cynipidae to one. This alternation of parthenogenetic with sexual reproduction is termed *heterogamy*. Certain kinds of young of the Psychidae, Tineidae, Coccidae and of numerous Hymenoptera (Apidae, Vespidae, Cynipidae, Tenthredinidae) and others also arise from eggs which have never been fertilized. The drones of the social colonies arise in this way. *Chermes* presents an example of heterogamy, two oviparous but different generations following one another in the course of the year. A winged form lasts through the summer and from its eggs a wingless form arises in the autumn and lives through the winter and is replaced by the first form again in the spring. In many species of *Chermes* the male is unknown. In certain species of Tenthredinidae, Coccidae and Cynipidae no male has yet been found, and as far as we know reproduction in these species is entirely parthenogenetic. In some insects

the unfertilized ovum always gives rise to one sex, it may be male or it may be female. In a few Diptera *paedogenesis* occurs, young being produced by a pupa or even by a larva.

The eggs laid by an insect vary in number from a few as in the Collembola and Psocidae to a million as in the Bee. They are usually deposited in water or on or near the food, which may consist of plants, animals or dung, on which the issuing larva

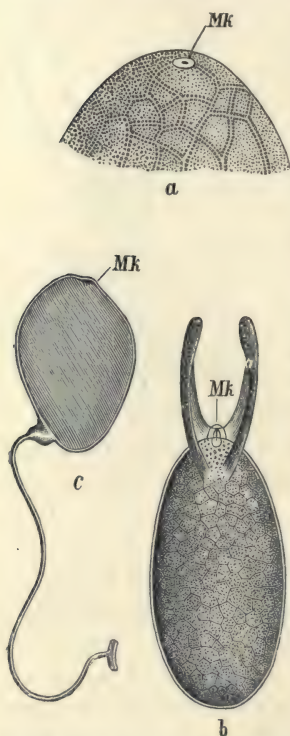


FIG. 400.—Micropyles (Mk) of insect eggs (after R. Leuckart). *a* upper part of the egg-shell of *Anthomyia*; *b* egg of *Drosophila cellaris*; *c* stalked egg of *Paniscus testaceus*.

lives. The cockroach shelters her eggs in a stout chitinous ootheca, the *Mantis* in a papery dome of hardened froth, the lace-winged Neuroptera protect their ova by supporting them on thin unclimbable stalks (Fig. 400, c), the Hymenoptera guard theirs in cells of wax or cement. The chief enemies to the eggs are certain species of ovivorous mites. The time of incubation varies from a few hours to, in the case of certain "walking-stick" insects (Phasmidae), two years.

The egg is as a rule large and contains much food-yolk. It is rounded, oblate or more usually oval, and the outer egg-shell or chorion may be much sculptured. The anterior end of the egg, that which will give rise to the head, lies—whilst the ovum is still within the ovaries—directed towards the head of the mother.

During the last few years the phenomenon of polyembryony or embryonic fission has been found to occur in the families Chalcididae and Proctotrypidae among the Hymenoptera. Naturalists have long been familiar with some remarkable facts connected with the life-histories of certain members of the former family, but it is mainly through the recent researches of Marchal* and of Silvestri† that it has been possible to give a correct interpretation of them. Marchal studied the biology of *Encyrtus fuscicollis*, a parasite of the

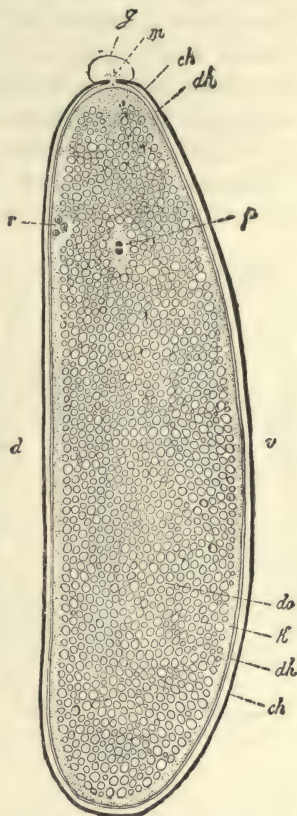


FIG. 401.—Diagrammatic median section through the egg of *Musca* at the stage of fertilization (taken from drawings by Henking and Blochmann). *ch* chorion; *d* dorsal side of the egg; *dh* vitelline membrane; *do* food-yolk; *g* glutinous cap over the micropyle; *k* peripheral protoplasm (periplasm or perivitellus); *m* micropyle; *p* male and female pronucleus before fusion; *r* polar bodies; *v* ventral side of the egg.

* *Arch. Zool. Exp. et Gén.* (4), ii, 1904, also *Bull. Soc. Vaud. Sci. Nat.* 1906, No. 153.

† *Rend. Acc. Lincei* (5), xiv, ii., p. 534.

larvae of moths of the genus *Hyponomeuta*, and it is in an egg of the latter that the *Encyrtus* deposits its own egg. By a remarkable process of nuclear fission a single egg of this parasite gives rise to over a hundred embryos, arranged in the form of a continuous chain, and lying in the body cavity of the larval host. The resulting larvae devour the organs of their host and pass into pupae under its now empty skin, and after a short interval the winged Chalcids emerge.

Silvestri has studied another member of this family viz. *Litomastix truncatellus*, which is similarly parasitic in the eggs

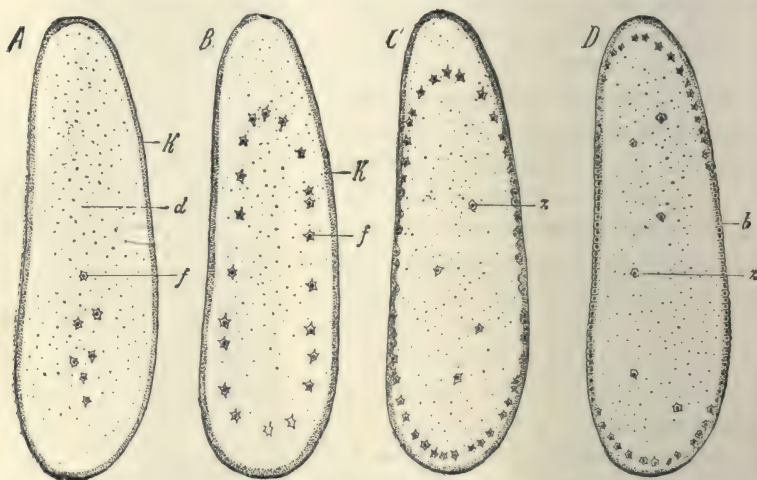


FIG. 402.—The formation of the blastoderm in *Hydrophilus* (after Heider). *b* developed blastoderm; *d* food-yolk; *f* so-called cleavage-cells; *k* peripheral protoplasm; *z* yolk-cells.

of the Noctuid moth *Plusia gamma*. In this case it was discovered that a single *Litomastix* egg produced about a thousand "sexual" larvae and a hundred or more "asexual" larvae within its host. The former alone are transformed into adults, the latter subsequently perish.

In the family Proctotrypidae Marchal has studied a species, *Polygnotus minutus*, which is parasitic in the larva of the "Hessian" fly (*Cecidomyia destructor*). In this instance the embryos resulting from the fission of a single egg seldom reach twelve in number.

In both families it has been ascertained that the winged parasites which emerge from a single host most often belong

to a single sex. At times, however, males and females come out in equal numbers, and this is to be explained on the grounds of the host containing more than one chain of embryos, since the parasite sometimes deposits more than one egg within that of its host. The phenomenon of polyembryony has a wide biological significance on account of its bearing on the problem of sex. Similar processes occur among the Polyzoa (Vol. I., p. 563).

Within the vitelline membrane which is secreted by the egg itself lies a layer of protoplasm, the *periplasm*, comparatively free from yolk; this surrounds a central mass in which the protoplasm

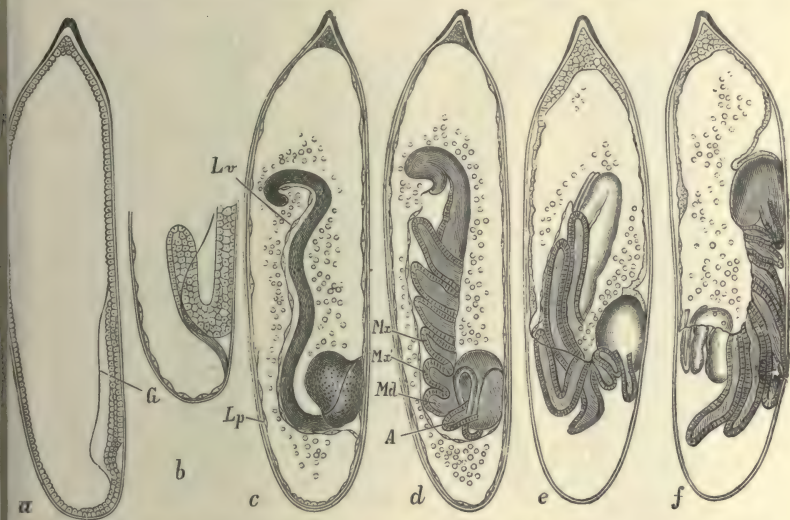


FIG. 403.—Embryonic development of *Calepteryx virgo* (after A. Brandt). *a* commencing involution of the ventral plate. The blastoderm was at first one-layered and thickened at the poles. *G* edge of ventral plate. *b* Later stage of the involution. *c* The embryonic membranes are developed; *Lp* parietal (serosa); *Lv* visceral (amnion) layer of the latter. *d* The appendages have sprouted out on the ventral plate. *A* antenna; *Md* mandible; *Mx* first maxilla; *Mx* second maxilla (labium or lower lip). Then follow three pairs of legs. *e* Eversion of the embryo which is protruded from the sheath of the visceral layer. *f* Completion of the inversion; the hind end of the body is free; the yolk sac is on the dorsal surface.

is scanty and crowded with food-yolk (Fig. 401). The nucelus lies in the central portion, but approaches the surface when mature, and then it gives off successively two polar bodies and, after receiving the male pronucleus, passes back as the cleavage nucleus again towards the centre of the egg. It then divides, and, when the products of division have reached a certain number, most of them approach the periphery and around each a certain cell-territory becomes marked off in the periplasm. Thus an

epithelium-like blastoderm is formed all over the egg. A few of the cleavage nuclei remain in the yolk and together with the protoplasm around them develop into vitellophags which help to liquefy the yolk and render it capable of being assimilated.

Very soon a differentiation appears along the ventral surface. The blastoderm cells there thicken to form the embryonic band and along the median line some cells are invaginated to form the "lower layer" which is destined to form ultimately

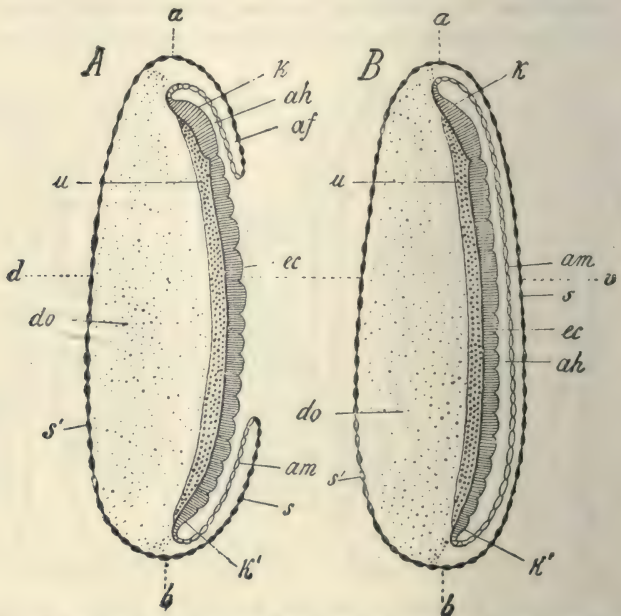


FIG. 404.—Two diagrammatic sagittal sections through an insect-embryo to illustrate the development of the embryonic envelopes. In *A* the germ-band (*k*, *k'*) is not completely grown over by the amniotic fold. In *B* the amniotic folds have united and completely cover the germ-band. *a* anterior, *b* posterior pole of the egg; *v* ventral; *d* dorsal; *af* amniotic fold; *ah* amniotic cavity; *am* amnion; *do* food-yolk; *ec* ectoderm; *k* cephalic end of the germ-band; *k'* posterior end of the germ-band; *s* part of the serosa derived from the amniotic fold; *s'* part of the serosa derived from the undifferentiated blastoderm; *u* lower layer. After Korschelt and Heider.

both mesoderm and endoderm. The dorsal epithelium has in the meantime become thinner and lies like a layer of flattened cells on the yolk. The embryonic band is not exposed. It may sink into the yolk in the manner indicated in Fig. 403 or more usually it is concealed by the upgrowth of an amnion as is shown in Fig. 404. The embryonic band at an early stage shows traces of segmentation corresponding with the somites of the

adult, and as a rule the development of the somites and their appendages takes place from before backwards. An anterior ectoderm invagination to form the stomodaeum and a similar insinking posteriorly to form the proctodaeum occur about the same time as the primitive limbs begin to project. The second of these limbs, the antennae, are at first postoral but soon shift in front of the mouth. In many developing insects rudiments of abdominal appendages have been seen, but these all disappear at an early age, excepting in the Collembola and Thysanura. The nervous system arises as an ectodermal thickening before the limbs appear and quickly undergoes a segmentation into ganglia. The tracheae arise as ectodermal invaginations, typically a pair in each segment of the body.

Whilst these various processes, more or less externally visible, have been going on, the embryonic band has been growing all along

its sides and thus gradually ensheathing the yolk. The larger part of the layer of cells which we have referred to above as the "lower-layer," becomes mesoderm, but anteriorly around the base of the stomodaeum and posteriorly around the base of the proctodaeum some of the cells of the "lower-layer" form the rudiments of the endoderm. These rudiments grow towards each other, forming two V-shaped bands which ultimately fuse and then broaden out, enclosing between them a large part of the food-yolk. The two bands first meet in the ventral line

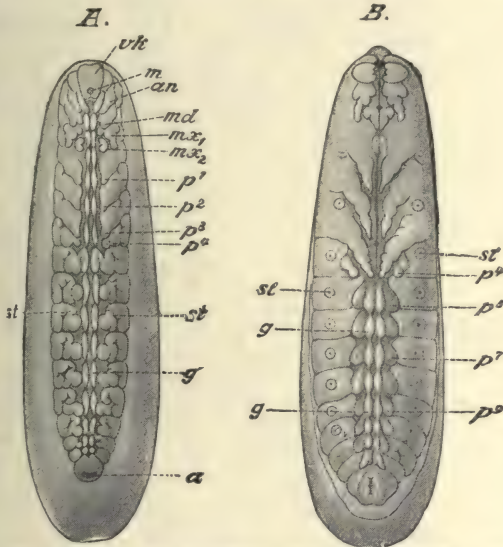


FIG. 405.—Embryos of *Hydrophilus* with limb-rudiments (after Heider, from Lang's *Text-book*). *a* anal aperture; *an* antenna; *g* rudiment of the ventral chain of ganglia; *m* oral aperture; *md* mandible; *mx*₁ first, *mx*₂ second maxilla; *p*¹, *p*², *p*³ the three pairs of thoracic limbs; *p*⁴, *p*⁵, *p*⁷, *p*⁹ rudiments of the first six abdominal limbs; *st* stigmata; *vk* procephalon.

and ultimately in the dorsal. By this time the yolk has come to lie completely within the alimentary canal. In some insects however the above account does not hold good. In them the

alimentary canal seems to arise entirely from the ectodermal invaginations of the stomodaeum and proctodaeum.*

The salivary glands arise as ectodermal invaginations and originally open on the exterior of the body but subsequently into the stomodaeum. The malpighian tubules arise as out-growths of the proctodaeum. In one or two genera, e.g. *Apis* they appear before the proctodaeum is formed and thus for a time open on the exterior.

What is left of the "lower-layer," after the separation of the endoderm rudiments before and behind, forms two bands, and segmental coelomic cavities appear along each band. These extend into the limbs and are better developed in the Orthoptera than in other groups of Insecta. The haemocoel of the Insecta has nothing to do with these coelomic cavities but is formed by the separating of

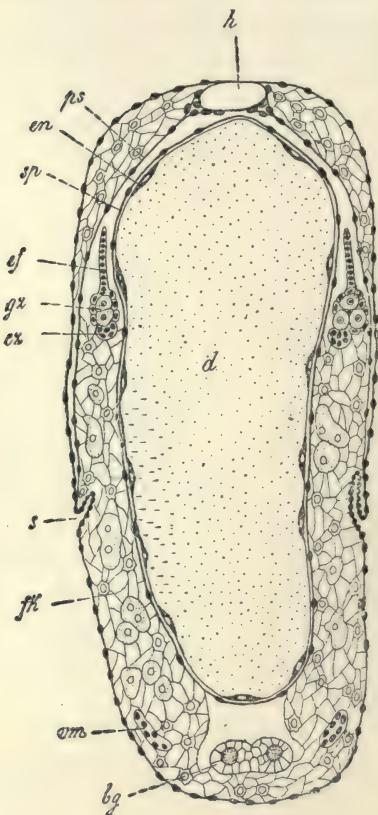


FIG. 406.—Transverse section through the abdominal region of an embryo of *Phylodromia germanica*, after the circumscrescence of the yolk and the formation of the dorsal surface are completed. *bg* ventral ganglionic chain; *cz* rudiment of the efferent genital duct; *d* food-yolk; *ef* terminal filament; *en* endoderm; *fk* tissue of the fat-body; *gz* genital cells; *h* heart; *ps* pericardial septum; *s* tracheal stigma; *sp* splanchnic mesoderm; *vm* ventral longitudinal muscle.

the embryonic band from the yolk and for a time is bounded by the yolk on one side and certain sparsely scattered mesen-

* Heymons, *SB. Ak. Berlin*, 1894, and *SB. Ges. Naturf. Berlin*, 1896; and Witlaczil, *Zeit. wiss Zool.*, xl, 1884, p. 559.

chyme cells on the other. The most dorsal edge of the somewhat triangular coelomic pouches gives origin to a row of *cardioblasts* or cells destined to form the walls of the heart. The pericardium arises a little later, also from the mesodermic cells.

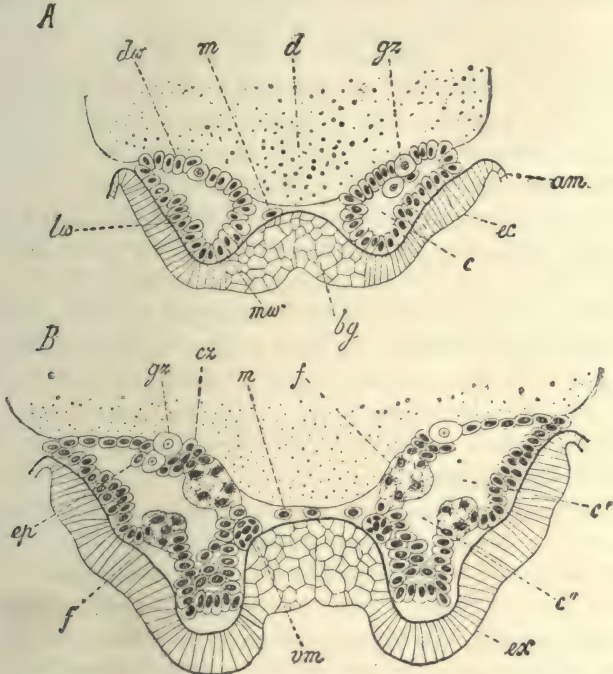


FIG. 407.—Transverse sections through the abdominal region of two consecutive stages in development of *Phyllodromia germanica* (after Heymons). *am* amnion; *bg* rudiment of the ventral chain of ganglia; *c* coelomic cavity; *c'* dorsal, and *c''* ventral portion of the coelomic cavity; *cz* cells of the primitive segments which become applied to the genital rudiment; *d* food-yolk; *ds* dorsal wall of the coelomic sac; *ec* ectoderm; *ep* epithelial cells; *ex* abdominal limb-rudiments; *f* rudiment of the fat-body; *gz* genital cells; *lw* lateral wall of the coelomic sac; *m* mesoderm-cells which do not take part in the formation of the coelomic sacs; *mw* median wall of the coelomic sac; *vm* ventral longitudinal muscle.

The muscles of the Insect body are differentiated from the cells of the somatic mesoderm, from which the fat body also originates.

The cells which form the reproductive elements are recognizable at an early stage, indeed, in the *Diptera* and *Aphidae*, before the blastoderm is definitely established. In other Insects they are conspicuous by their large size lying in the splanchnic wall of the coelomic sacs from the second to the seventh abdominal

somites (Fig. 407). They later shift into the lumen of the sac, the dorsal wall of which forms the terminal filament of the reproductive gland. The cells from neighbouring sacs ultimately become contiguous and the investment of the gonad is derived from adjacent mesodermic cells.

Metamorphosis. The egg of an Insect gives rise to a creature which always differs more or less from the adult, and in many cases the difference is so great, that, unless we knew their life-history, we should hardly class the larvae amongst the Insecta. The typical number of segments for the species is however always found in the larva, so the difference between young and old is not so marked as between such a larva as a nauplius and the form it gives rise to. In many orders, which in certain features of the development most closely resemble the Myriapods, the change from larva to adult is comparatively gradual. The animal undergoes a series of ecdyses and after each casting of the skin it approximates a little more closely to the final form. Such a series of small steps is termed *incomplete metamorphosis*. In the remaining orders, the larva differs more or less markedly in structure and in habit from the adult.

It has been thought that in some groups such as the Thysanura no metamorphosis whatever occurs, and that the young are simply miniature copies of the adults, and merely increase in size during development. These insects were called *Ametabola*. But Heymons* has recently shown that there is a slight metamorphosis even in some of the most primitive Thysanura. He concludes that apart from a few exceptional cases no such thing as true ametaboly exists in the Insecta, but that all undergo some metamorphosis. He proposes the division of the class into two categories.†

(i) **Epimorpha**, in which the young differ from the adults

* Heymons, Über die ersten Jugendformen von *Machilis alternata* Silv., S. B. der Ges. Naturforsch. Freunde, Berlin, 1906 (Dec.), pp. 253-256. Heymons' views are elaborated in an important paper in Spengel's *Ergebnisse und Fortschritte der Zoologie*, Jena, i, 1907, pp. 137-188.

† Insects are also often divided into forms with incomplete metamorphosis or *Homomorpha*, and those with complete metamorphosis or *Heteromorpha*. The correspondence of these groups with those adopted by Heymons is shown thus:—

	Epimorpha	
Homomorpha = {	Hemimetabola	} Metamorpha.
Heteromorpha = {	Holometabola	

only by the incompleteness of their organization, and change gradually by a series of moults into the adult form.

(ii) **Metamorpha**, with a definite larva the structure of which is in many ways completely different from that of the adult, and with a more or less complete transformation from young to adult.

I. The **Epimorpha**.

The young resemble the adult on the whole in habit and structure. No special larval organs are developed. This group includes the Collembola and Thysanura, and the Mallophaga, in which the differences between young and adult are only very slight; consisting, for example, in the young having no external genital structures, and a less number of antennal joints than the adult. It also includes orders in which the young differs from the adult by the absence of wings, which develop gradually at successive moults. These are the Dermaptera, Orthoptera, Termitidae, Psocidae, and Hemiptera.

II. The **Metamorpha**.

A definite larval stage is present. This category is further divided, according to the degree of the transformation exhibited in changing from larva to adult, into:—

(a) **Hemimetabola**. Insects without the definite resting stage known as the *pupa*.

(b) **Holometabola**. Insects with a definite pupal stage.

(a) The **Hemimetabola** include certain orders in which the young differs from the mature insect or *imago* not only in the absence of wings but in the possession of certain larval organs which later disappear. The habits of larva and adult are often very different. To this group belong the Odonata and Plecoptera.* The larvae are in these cases aquatic and breathe by external gills or by tracheal folds of the rectum, which disappear at the last ecdysis. The stage which precedes the imago and in which the process of transformation takes place is frequently called the *nymph*. Although in this stage the insect often becomes for some time quiescent, yet there is no definite pupa.

* In the second of Heymons' papers referred to previously, he places the Ephemeridae in an independent division (*Prometabola*) of the Holometabola, owing to their having a winged and active sub-imago stage between the pupal and imago stages.

(b) The **Holometabola** have both a definite larval and pupal stage. They are said to undergo *complete metamorphosis*. The larva takes in a relatively enormous amount of nutriment, to accommodate which it frequently moults. Finally it changes into the almost motionless pupa. This takes no nourishment, but within it the body of the insect is reconstituted into the imago. This group includes the orders Siphonaptera, Neuroptera, Panorpidae, Trichoptera, Lepidoptera, Coleoptera, Strepsiptera, Diptera and Hymenoptera. A certain amount of the reconstruction takes place also in the late larval stages.

The *larva* differs markedly from the imago both in structure and habits. It is impossible within our limits to describe the various forms which larvae assume. In the main the form is adapted to obtaining the food which they—the pre-eminently food-absorbing stage of insect life—eat. The characters of the various larvae are on the whole secondary, and have but little value as guides to phylogeny. Some larvae are to a great or less extent simplified and have lost their locomotor appendages and their mouth-parts.

Roughly speaking larvae fall into two categories. The first is the so-called *Campodeiform* larva named after the Thysanuran *Campodea*, and has the three primary regions or tagmata, head, thorax and abdomen well defined, thoracic walking legs, primitive biting mouth parts, and sometimes terminal appendages on the abdomen. Such creatures may be found among Holometabola, *e.g.* larvae of certain Coleoptera, but the characteristic larval stage of Holometabola is the *Eruciform* larva, of which the best known example is the Caterpillar. The skin is usually thin, the body somewhat vermiform, the tagmata of the body not well defined though the head is clearly marked off, the mouth parts are often biting but may be much reduced, thoracic limbs usually occur, and less frequently also ambulatory appendages or *pro-legs*. The eruciform larva is typically developed in the Lepidoptera, and in the Saw-flies among the Hymenoptera; in other Hymenoptera and in many Diptera it has lost many of its characters, the legs and mouth-parts are reduced or absent, the head very greatly reduced (some Diptera), and the larva is familiarly known as a grub or maggot. The number of ecdyses is often comparatively few; whereas in the larvae of Hemi-

metabola it may be high, in Ephemeridae sometimes as many as twenty.

The *pupa* resembles the imago much more closely than does the larva. It may be exposed or enclosed in a cocoon. The limbs of the pupa may stand out freely from the body as in the Coleoptera, when it is known as *free (pupa libera)*; or the limbs and wings, very soon after the emergence of the pupa from the last larval skin, may be glued to the side by a hardened secretion as they are in the Lepidoptera, when the pupa is called *obtecta*; or finally, as in many Diptera, the pupa may remain enclosed in the last larval skin, a condition known as a *pupa coarctata*.

The larval body of those insects with incomplete metamorphosis grows gradually into the body of the adult. Apart from wear and tear, the tissues of the one become in time the tissues of the other and the new organs such as the wings and the genital armature are formed by simple growth. In the insects with complete metamorphosis this is not the case. Traces of the imago are clearly discernible in the later phases of the larval stage, but when this ceases to move and to feed and turns into the inactive pupa a profound reorganization takes place in the body of the insect. A few of the systems of organs persist from the larva to the imago and these are amongst the most important such as the reproductive, the nervous and the circulatory. The other organs however are disintegrated. At the beginning of metamorphosis certain toxins* are said to arise in the blood which seem to poison certain definite tissues and cells, which then readily fall victims to the phagocytes. Each toxin seems specific to one set of organs, and the toxins arise in a definite sequence. The alimentary canal with its associated glands, the respiratory system, the fat-bodies, the epidermis and most of the muscles are destroyed and replaced by new growths. The active agents in this process of disintegration, known as *histolysis*, are the blood corpuscles. These become vigorously phagocytic and attacking the component cells of the fated organs gradually break them up and absorb them. At the same time new organs arise to play the same parts in the imagines as did the evanescent organs in the larva. And they arise at special foci or centres which are known as *imaginal discs*. These are collections of cells which seem to have retained

* S. Metelnikoff, *Biol. Centrbl.* xxvii. 1907, p. 396.

an embryonic power of growing into new organs. Their number varies in different families and probably reaches a maximum in the Diptera. In the Lepidoptera the head with its mouth parts and the thoracic legs of the caterpillar pass with some modifications direct into the corresponding parts of the moth, but the compound eyes and the wings arise from imaginal discs. In the Diptera however there are always imaginal discs for each of the legs and in many cases, i.e. the *Muscidae*, special discs for the reconstitution of the head. The whole epidermis is also renewed, a layer of new cells arising around the base of the limbs and

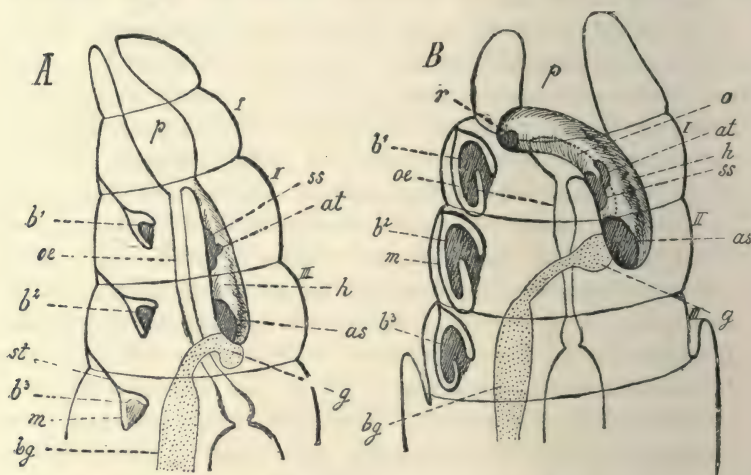


FIG. 408.—Diagrams illustrating the position of the imaginal discs in the larva (A) and pupa (B) of *Musca* (taken from Van Rees). The wing-rudiments are omitted. *as* optic disc; *at* antennal rudiment; *b*¹, *b*², *b*³ rudiments of the three thoracic limbs; *bg* ventral chain of ganglia; *g* brain; *h* so-called "brain-appendage"; *m* peripodal membrane; *o* aperture of the brain-appendage into the pharynx; *oe* oesophagus; *p* so-called "pharynx"; *r* rudiment of the proboscis; *ss* frontal disc; *st* stalk-like connexion between the peripodal membrane and the hypodermis; *I*, *II*, *III* the three thoracic segments.

insinuating itself between the cuticle and the larval epidermis. The latter is finally destroyed by the phagocytic activity of the blood-corpuscles. In the abdomen there are four imaginal discs in each segment destined to form new epidermis. Other centres form the muscles of the adult which replace the disintegrated bundles of the larva. The stomodaeal and proctodaeal portions of the intestine are reconstituted from ring-like imaginal discs which occur at the inner end of these invaginations, and numerous imaginal discs occur along the course of the alimentary canal. These growing and finally fusing with one another

gradually ensheath the lining epithelium of the larval digestive tract. This epithelium is finally split off and lies in the lumen of the newly formed enteric tube.

The respiratory system undergoes a similar process of dissolution and reformation. The stigmata and the larger tracheae of the imago correspond neither with those of the larva nor with those of the pupa, but the system is at no one moment totally destroyed and it continues to function throughout the pupal life. The larval fat-bodies also undergo histolysis and are reconstructed from certain imaginal discs.

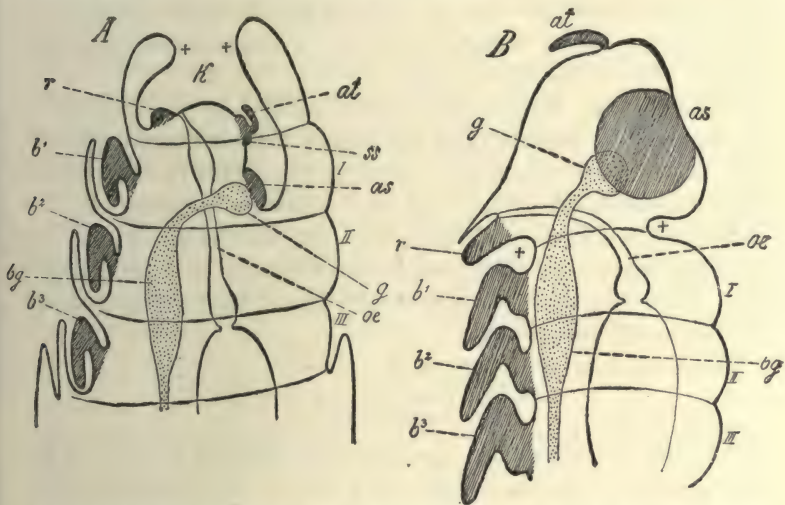


FIG. 409.—Diagram illustrating the transformations that take place in the pupa of *Musca* before it hatches (adapted from Kowalevsky and Van Rees). The wing-rudiments are not drawn. *as* optic disc; *at* antennal rudiment; *b*¹, *b*², *b*³ rudiments of the three thoracic limbs; *bg* ventral chain of ganglia; *g* brain; *k* cephalic vesicle (formed by the union of the pharynx with the brain appendage); *oe* oesophagus; *r* rudiment of proboscis; *ss* frontal disc; *I*, *II*, *III* the three thoracic segments.

The phagocytes of the blood which are the active agents in the dissolution of the various tissues, do not themselves form constituent parts of the new system of organs. They however doubtless act as distributing agents for the nutriment they have absorbed. Some of them become the blood corpuscles of the imago, but many of them degenerate and are finally absorbed within the newly formed tissues of the adult.

No evidence has been obtained of the existence of Insects before the Carboniferous epoch. In the coal measures they

are well represented. The best preserved specimens are found in the amber of the Oligocene in mid-Europe; in this specimens allied to *Lepisma* occur. Earwigs first appear in the Lias, cockroaches in the Trias and generalized locusts and grasshoppers in the coal-measures. This formation also contains a number of forms of Termites, Ephemerids, Dragon-flies. Beetles are found first in the Trias and become common in the Jurassic and Tertiary beds, in which the Cicadidae and Notonectidae are also met with. Butterflies and moths are found in the Jurassic strata but are amongst the rarest of Insect fossils. A few Diptera are found in the Lias and in the Oolitic Solenhofen Limestone, they become more numerous in the Tertiary strata and the same is true of the Hymenoptera.*

Classification. Insects are classified mainly on three features : (i) the absence, presence and the nature of their wings ; (ii) the structure of their mouth parts ; and (iii) the degree in which they undergo metamorphosis.† In the following account of the classification the large groups are in the main based on wing-characters, but these run to some extent on lines parallel with those laid down by our knowledge of the metamorphosis of the insects concerned.

There are four main groups : ‡

I. APTERYGOTA.

Wingless insects whose ancestors are believed to have been also wingless. Metamorphosis very slight. This group includes but two Orders, the (1) *COLLEMBOLA* and the (2) *THYSANURA*.

II. ANAPTERYGOTA.

Wingless insects supposed to have developed from winged ancestors. They are all parasitic on vertebrate animals. This group includes the Orders (3) *MALLOPHAGA* and (4) *ANOPLURA* in which the metamorphosis is very incomplete and the (5) *SIPHONAPTERA* in which the development is rapid and the metamorphosis complete.

III. EXOPTERYGOTA.

Winged insects whose wings develop outside the body and

* H. Woods, Palaeontology, Invertebrata, 1902.

† *Instar* is the term applied to the form of an insect between two moults (Sharp, *op. cit.*, i, p. 158).

‡ D. Sharp, Proc. International Congress of Zoology, Cambridge, 1898.

are never tucked or invaginated into the body. This group varies much in the degree to which metamorphosis is present; sometimes it is almost absent, and sometimes it is complete.

The group includes the Orders (6) *ORTHOPTERA*, (7) *PLECOPTERA* (*PERLIDAE*), (8) *PSOCOPTERA* (*PSOCIDAE*), (9) *ISOPTERA* (*TERMITIDAE*), (10) *EMBIOPTERA* (*EMBIIDAE*), (11) *EPHEMPTERA* (*EPHEMERIDAE*), (12) *PARANEUROPTERA* (*ODONATA*), (13) *THYSANOPTERA*, (14) *HEMIPTERA*.*

IV. ENDOPTERYGOTA.

Winged insects whose wings arise as invaginations of the hypodermis and for a time project inside the insect's body, but are subsequently evaginated. Complete metamorphosis exists. This group is by far the largest and perhaps contains at the present day some ninety per cent. of the total number of insects. It is probably descended from the Exopterygota, which—with one or two exceptions—were the insects of the Palaeozoic epoch. The group includes the Orders (15) *NEUROPTERA*, (16) *MECAPTERA* (*PANORPIDAE*), (17) *TRICHOPTERA*, (18) *LEPIDOPTERA*, (19) *COLEOPTERA*, (20) *STREPSIPTERA*, (21) *DIPTERA* and (22) *HYMENOPTERA*.

Group I. APTERYGOTA.†

Wingless insects believed to have descended from wingless ancestors. Metamorphosis very incomplete.

Order 1. COLLEMBOLA.‡

Minute wingless insects; abdomen of no more than six visible segments; a protrusible papilla or blind tube borne on the first abdominal segment; a jumping mechanism often present.

The Collembola are for the most part soft-bodied insects covered with a hairy down or bloom. Their spring consists of a median piece bearing a pair of processes. The whole arises from the penultimate or ante-penultimate segment (Fig. 410, b). In dead specimens the processes project backward, but during

* Shipley, *Zool. Anz.*, xxvii, 1904, p. 259.

† J. Philpitschenko, *Zeitschr. wiss. Zool.*, lxxxviii, 1907, p. 99.

‡ Lubbock, *Monograph of the Collembola and Thysanura*, Ray Society, 1873.

life they can be bent forward under the abdomen and are then held in position by a "catch" which is carried on the third abdominal segment. If the catch be released the downward

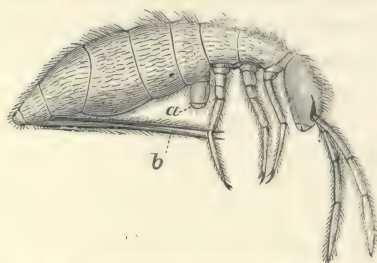


FIG. 410.—*Corynothrix borealis*. *a* ventral tube; *b* the spring (after Tullberg).

blow of the processes projects the insects suddenly into the air. The catch only exists in certain species, and this explanation of the action of the springing apparatus is not universally accepted. The second structure peculiar to the Collembola is the ventral protrusible organ of the first abdominal segment (Fig. 410, *a*).

This in the Lipuridae and Anuridae is little more than a protrusible papilla, in the Smynthuridae, however, it is a long, caecal tube which splits into two limbs near its base. Its function is a matter of dispute, but the usual view is that it is an organ for attaching the small insect to a desirable spot. Development shows that the ventral tube, the catch and the spring are formed from the embryonic appendages borne on their respective segments. The remaining three abdominal segments lose their appendages.

The tracheal system is often reported as absent, but *Smynthurus* is described as having a pair of stigmata situated between the head and the prothorax; a very unusual position.* The mouth parts are withdrawn into the head. Some authorities consider that there is an extra or fourth pair of "jaws," the maxillulae, † and although this view is not universally accepted the mandibles are regarded as very archaic in structure. The antennae have but four to six segments and at their base is a post-antennal sensory organ. The legs have no tarsus, the tibia simply ending in one claw or in two unequal claws.

The spring-tails, as the Collembola are often called, when they do occur, usually do so in great numbers. They mostly haunt concealed retreats, hiding under bark, stones, etc. Some are aquatic e.g. *Podura aquatica*, which sometimes occurs in

* Willem, Recherches sur les Collemboles et les Thysanoures; *Mem. Cour. l'Acad. Sc. Belg.*, T. lviii, 1900.

† H. J. Hansen, *Zool. Anz.*, xvi, 1893; *op. cit.* on p. 604; see also p. 605.

incredible numbers after floods; others, as *Anurida maritima*,* are marine, living on the water of rock pools along our coast. When the tide rises they retire to crevices in the rocks, but they can survive long periods of immersion. A considerable number of species have been taken in both Polar regions and they are common on snow and glaciers, which at times are blackened by their countless numbers. The group is practically cosmopolitan, though they seem on the whole to avoid warm districts. They are said to live on organic débris of all kinds. Lubbock recognized six families, but these have more recently been reduced to three :—

Fam. 1. **Smynthuridae**. Bodies globular, devoid of scales and with a considerable fusion of segments; the apparent thorax small; antennae elbowed; spring borne by fifth abdominal segment; tracheal system present. This family includes the Smynthuridae and Papiiidae of Lubbock. Many of the members haunt bushes and undergrowth. *Smynthurus*; *Papius*.

Fam. 2. **Poduridae**. Elongate bodies not swollen; spring on fourth abdominal segment or in the Degeerides (= Lubbock's family Degeeridae) on the fifth. These forms somewhat resemble minute caterpillars and are often highly coloured. *Podura*; *Isotoma*; *Corynothrix*.

Fam. 3. **Lipuridae**. No spring. Slowly crawling minute creatures. This includes the Lipuridae and Anouridae of Lubbock. *Anoura* has very much modified mouth-parts, and its mouth is described as suctorial, whilst that of *Lipura* is mandibulate.



FIG. 411.—*Podura villosa*.

Order 2. THYSANURA. †

The abdomen shows ten segments and there is no ventral protrusible tube or springing apparatus; wingless; with long multi-segmented antennae and sometimes compound eyes. Cerci anales on last abdominal segment.

The Thysanura, sometimes termed "bristle-tails," are insects of moderate size. They have no trace of wings, and the prothorax is often the largest segment in the body. Usually they move actively, and tarsi are present on the legs. The abdomen

* *Anurida*, A. D. Imms, *Liverpool Marine Biological Committee Memoirs*, xiii, 1906.

† Grassi, *Mem. Acc. Lincei Rome* (4), iv, p. 543, 1888; and Oudemans, *Bijdr. Dierkunde*, xvi, p. 147, 1888. Escherich, *Zoologica*, Heft xliii. Silvestri, *Zool. Jahrb. Suppl.* vi, 1905, p. 74.

consists of ten visible segments and the last bears a pair of many segmented cerci which superficially resemble antennae. Certain of the abdominal segments bear on the hinder edge of their sterna

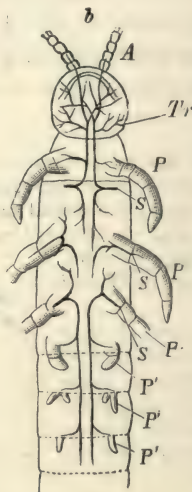


FIG. 412.—*a* *Campodea staphylinus* (after J. Lubbock).
b anterior half of the body of *C. fragilis* (after Palmén); *Tr* trachea; *S* stigmata; *P* legs; *P'* rudimentary abdominal feet; *A* antennae.

small appendages articulated with the ventral surface. They consist of a single segment provided with muscles. By many authorities these appendages are regarded as homologous with the legs, but it must not be forgotten that both legs and processes exactly similar to those borne by the abdomen co-exist on the meso- and meta-thorax of *Machilis*. Close to the insertion of some of these processes are one or two retractile vesicles which can be protruded by the intrusion of blood or retracted into the body by muscular action.

They appear to function as accessory respiratory organs. What are regarded as a fourth pair of jaws (maxillulae) are present as in Collembola. In *Japyx** they are described as being very primitive and divisible into galea, lacinia and a three-jointed palp (Fig. 372).

There are four families, in two of which the mouth is pushed into the head carrying the mouth-parts with it. These two families, the Campodeidae and the Japygidae, are sometimes classed together as the Entotrophi, and the remaining families, the Machilidae and the Lepismidae, in which the mouth parts are prominent are grouped as Ectotrophi.

* Hansen, *loc. cit.*

Fam. 1. **Campodeidae.** Delicate, white insects with long cerci; blind; mouth-parts concealed; abdominal appendages on the second to the seventh segments. Authorities differ as to whether there is more than one genus *Campodea* and as to whether that genus contains more than one species *C. staphylinus* (Fig. 412). This is a widely distributed insect, not uncommon in Britain; it well withstands heat and cold but variations in humidity seem to affect it and it soon dies in captivity. It is so delicate that it breaks at the slightest touch. Many of the features of this insect are archaic in character. The thorax has three pairs of stigmata, each leading into a separate system of tracheae, which systems do not communicate with each other or their neighbours. There are sixteen very short malpighian tubules. The appendages of the third true segment, the intercalary, are said to persist as tubercles in the adult. The ovaries and testes are two simple tubes one each side of the body.

Fam. 2. **Japygidae.** The abdomen bears a pair of forceps instead of long multi-segmented cerci; abdominal appendages on first to seventh segment (Fig. 369A); mouth parts concealed. The single genus *Japyx* with several species is widely distributed in the warmer parts of the globe. There are four thoracic and seven abdominal pairs of stigmata and the tracheal system of one segment opens into that of the others. No malpighian tubules. The female generative organs are metamerically repeated, the ovaries uniting into a common oviduct on each side. The testes however have lost this segmental arrangement. Only one pair of abdominal vesicles have been described. *Japyx* is usually found in shady places on the edge of woods, etc., but it does not occur so far north as Britain.

Fam. 3. **Machilidae.** The tergites arch over and overlap the ventral sternites in the abdomen much as in *Astacus*; compound eyes are present; the female has an ovipositor and the tenth abdominal segment bears a long median structure resembling the cerci and projecting between them.

There is again but one genus *Machilis* with two pair of thoracic and seven pair of abdominal stigmata, which open into nine isolated tracheal systems. There are twenty long malpighian tubules and also diverticula which open anteriorly into the stomach. The seven ovarian tubules on each side are not very definitely segmental. The abdominal appendages are found on segments two to nine inclusive. The body bears numerous scales very easily displaced. *Machilis* is cosmopolitan in distribution. *M. maritima* is common, running about the rocks on the south of England, and *M. polypoda* lurks under leaves in the New Forest and elsewhere.

Fam. 4. **Lepismidae.** The thorax well marked off from the abdomen; tracheal systems all intercommunicate; the tergites do not overlap the sternites; abdominal appendages on eighth and ninth segments only; a median "tail" as in *Machilis* between, and as long as, the cerci. The Lepismidae have ten pair of stigmata and the tracheae communicate one with another. The number of malpighian tubules is small. There are



FIG. 413.—*Lepisma saccharina*

five ovarian caeca which in the young are segmentally arranged as are the three pair of caeca which make up the testes on each side. The family is a widely distributed one, the best known British form being *Lepisma saccharina* (Fig. 413), the "silver-fish" which is found only in or near human dwellings, in old cupboards, sugar barrels, etc. The other British Lepismid is *Thermobia furnorum*, which lives in bake-houses.

Group II. ANAPTERYGOTA.

Wingless insects whose ancestors probably were winged. Parasitic on Vertebrates. The first two Orders with very slight metamorphosis, the third with complete metamorphosis.

Order 3. MALLOPHAGA.*

Wingless with flat bodies and large heads; prothorax distinct, the meso- and meta-thorax small and the latter often fused with abdomen.

The insects of this order are usually termed Bird-lice, but as they do not live exclusively on birds the term Biting-lice has been recently substituted. They live amongst the feathers of birds or the hairs of mammals, crawling about the bases of these epidermal structures. Their bodies are flattened and their heads exhibit a great variety of shape. The antennae are short with but three

to five segments; the eyes are reduced or absent; the mandibles toothed, the first maxillae are mere lobes which are said to bear no palps, the second maxillae or labium have in two families well-developed palps, but these are absent in another subdivision. The segments of the abdomen which are apparent, vary in number from eight to ten. The legs have usually a one- or two-segmented tarsus; rarely three segments occur; the tarsi end in one or two claws, and in the former case the claw is especially fitted to the hair of the animal which harbours the insect.



FIG. 414.—*Menopon pallidum*; inhabits the common fowl, *Gallus domesticus* (after Piaget).

The ventral nerve cord is concentrated in the thorax there being no abdominal ganglia. The ova are laid amongst the hairs or feathers. The young resemble their parents very

* Giebel and Nitzsch, *Insecta Epizoica*, 1874. Grosse, *Zeitschr. wiss. Zool.*, xlii, 1885, p. 530. Melnikow, *Arch. Naturg.* xxxv, 1869, p. 154.

nearly. These creatures live on the younger and more succulent portion of the feathers of birds and possibly on the hairs and epidermal scales of mammals, and are said to use their anterior legs in feeding. There is as a rule a certain relationship between the species of the biting-lice and the species of its host, but certain birds are infested by more than one species, e.g. the common fowl has five. They often die soon after their host. There are about a thousand species recorded.

Howard recognizes four families :—

Fam. 1. **Trichodectidae**. Antennae filiform with three joints; no labial palps; tarsi with a single claw; infest mammals. *Trichodectes latus* is the biting-louse of the dog. *T. sphaerocephalus* is one of the common sheep parasites in England.

Fam. 2. **Philopteridae**. Antennae five-segmented; no labial palps; tarsi with two claws; infest birds, *Nirmus*, *Goniodes*.

Fam. 3. **Gyropidae**. Antennae clubbed with four segments; tarsi with one claw; found on mammals. *Gyropus*.

Fam. 4. **Liotheidae**. Antennae clubbed with four segments; tarsi with two claws; infest birds. *Tetraphthalmus*.

Order 4. ANOPLURA.*

Small, thin-skinned insects; wingless; head bears a tube ending in hooks for attachment, within this is a portrusible sucking tube; thorax indistinctly segmented; legs end in a single claw.

Lice are parasitic on Mammals on whose blood they live. In spite of the fact that three species infest man we are curiously ignorant of many features of their life history and of their structure.

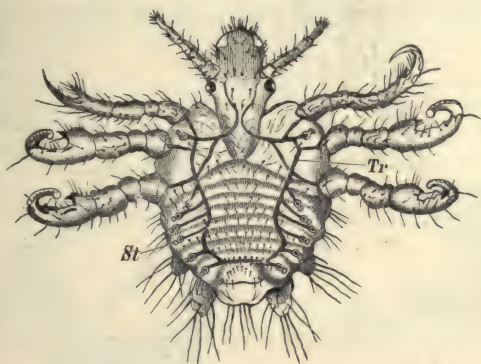


FIG. 415.—*Phthirus inguinalis* (after Landois). *St* stigma
Tr trachea.

The tube by which they attach themselves to the skin is usually homologized with the labium whilst the inside tube is looked upon as the equivalent of the combined mandibles and maxillae.

* E. Piaget, *Les Pediculines*, Leyden, 1880-85.

A labrum is also described. Meinert however holds, with much appearance of reason, that the inner, protrusible tube is modified from the epi- and hypo-pharynx.* As in the Mallophaga the nervous system is much concentrated. There is but one family:—

Fam. 1. **Pediculidae**. With the characters of the Order. There are six genera and about forty species of Lice, three of which *Pediculus capitis*, *P. vestimenti*, and *Phthirus inguinalis* (Fig. 415) attack man. Many authorities regard the first two as one species. They still form a terrible scourge to armies in the field, but are far less common than in the middle ages, when especially in the South of Europe most inns kept a lousing-room or outhouse, described in many a Spanish novel. Monkeys suffer much from a distinct genus *Pedicinus*, Seals are infested by *Echinophthirius* and Elephants by *Haematomyzus elephantis*. The claw which terminates each leg is said to be beautifully adapted in the various species to the circumference of the hairs of their respective hosts.

Order 5. SIPHONAPTERA † (APHANIPTERA).

Laterally flattened insects, without wings; head small with short stout antennae; no neck; eyes small or absent.

The flattening of the body in the vertical, longitudinal plane is confined to the flea amongst insects. The antennae have a



FIG. 416.—a *Pulex avium* ♂ (after Taschenberg). A antenna; Mt maxillary(palp. b larva of *Pulex irritans*.

peculiar insertion and are often placed in depressions; there seems to be no clypeus, the mandibles are piercing stylets with saw-like edges, the maxillae bear long palps which project and

* Meinert, *Ent. Meddel.* iii, p. 58, 1891.

† Taschenberg, *Die Flöhe*, 1880. Wagner, *Horae Soc. ent.*, xxiii, 1889, p. 199. N. C. Rothschild, *Nov. Zool.* v, 1898, p. 533 and *Rep. Thompson Yates and Johnston Lab.*, vii, 1906, p. 1.

are often taken for antennae (Fig. 416). The labium is thought by some authorities to be represented by an unpaired median stylet, but others regard this as a hypopharynx; the labial palps are semi-segmented and form two sheaths which enclose the piercing organs. Ten pair of stigmata exist both in the larva and the imago. The eggs are laid amongst the hair of the host but not attached to them, so that they readily fall off and the young are reared amongst the dust under carpets and in like retreats. The larvae (Fig. 416) are something like miniature white wire-worms (i.e. the larvae of Elaterid beetles), and they have a mandibulate mouth. They eat all sorts of dusty refuse but can be reared on moist bread crumbs. Before pupating they make a cocoon often covered with dust. There are about a hundred described species some of which seem confined to special hosts, but there is much divergence of opinion as to how far one species of flea migrates from one species of host to another. The rat flea of India which conveys the plague from rat to rat undoubtedly at times attacks man and is an active agent in infecting man with the disease. It is not uncommon to find disused houses swarming with fleas in such numbers that they can almost be swept up with a broom, hence it seems clear that a host, although desirable, may be absent at any rate for some considerable period of the life-history. Two families are recognized :—

Fam. 1. Pulicidae. The labial palps imperfectly divided into three to five segments; abdomen elongated and not greatly swollen in the female with ova. A cosmopolitan family: *Pulex irritans* is the human flea, *P. avium* infests birds, *P. serraticeps* dogs and cats. The last named species is said to be an intermediate host of the Cestode *Dipylidium caninum*. There are many other genera.

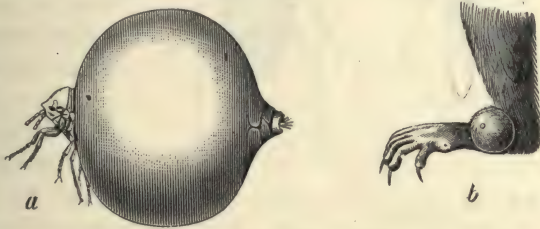


FIG. 417.—a Gravid female of *Sarcopsylla penetrans*. b foot of a field mouse with a *Sarcopsyllid* attached (after H. Karsten).

Fam. 2. Sarcopsyllidae. The labial palps have ten imperfect segments; abdomen short and in the fertilized female enormously swollen. This family includes the Jigger or Chigoe flea, *Sarcopsylla penetrans* (Fig. 417), the

fertilized female of which burrows in the skin of man, usually in the foot, and swells to the size of a dried pea. Then it discharges its ova. If not removed it causes trouble not only by its mere presence but by the introduction of bacteria into the deeper tissues. The Jigger is a native of the warmer parts of America, but has spread to Africa and elsewhere. In places it is a terrible pest, but it can be partially avoided at any rate by never putting the bare foot upon the ground. *S. gallinacea* attacks the eyelids of poultry in Ceylon, and *Rhynchopsylla pulex* the same parts of birds and bats in S. America.

Group III. EXOPTERYGOTA.

Winged insects whose wings develop outside the body. The degree of metamorphosis varies between fairly wide limits.

Order 6. ORTHOPTERA.*

Insects with biting mouth parts, with conspicuous maxillary and labial palps. Mesothoracic wings stiff, metathoracic wings membranous and closing like a fan, both pairs not infrequently absent or reduced in size. The adult form is attained by a series of small changes accompanying the successive ecdyses. There is no abrupt metamorphosis.

The Orthoptera form a large order containing at a low estimate 10,000 species. It is at the

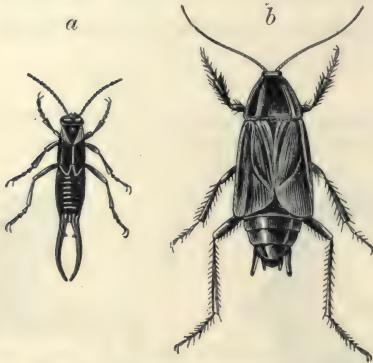


FIG. 418.—a *Forficula auricularia*; b *Blatta orientalis* ♂.

same time rather a heterogeneous assemblage, and it is not always possible to recognize at a glance an Orthopteron. The Order is large in another sense for it contains the biggest existing insects and even its smallest representatives attain a fair size. That there is considerable diversity of form is shown by the following list, which with some other forms

having no popular names, composes the Order:—earwigs, cockroaches, the praying-mantis, stick-insects, leaf-insects, grasshoppers, locusts and crickets.

* E. Shaw, *Ent. Mon. Mag.*, xxv, 1889, and xxvi, 1890. Brunner von Wattenwyl, *Ann. Mus.*, Genova, xxxiii, 1893, p. 5.

The anterior wings of the Orthoptera, sometimes called the *tegmina*, are not used for flight. They are stiff and tough, and when at rest lie flat on the body, which they serve to protect. In this position one overlaps the other, and their hinder (when closed, median) borders do not form a straight suture as is the case with the Coleoptera. The nervures of the hinder wings radiate from the point of attachment of the wing like the sticks of a fan, and they are connected with one another by short cross-nervures forming a network over the whole wing. These hind-wings are the organs of flight, but flight is an exercise little practised by Orthoptera. In some cases the wings are well developed but apparently unused, in others they are modified into sound-producing organs, and in others again they are absent, apterous forms occurring in all the families.

These feeble powers of flight are to some extent compensated for by the powerful legs, which enable certain Orthoptera to leap prodigious distances or to run with extreme rapidity; also it must not be forgotten that some species have specially powerful flight, e.g. the migratory locust.

The antennae are usually long, with many articulations: ocelli are usually present in addition to the large compound eyes. The three thoracic segments are not fused with one another, and the prothorax is freely movable. Ten segments can usually be made out in the abdomen, the anus being on the tenth and the genital orifice upon the ninth. The end of the abdomen may bear a pair of cerci in either sex; anal styles may be present in the male, and a powerful ovipositor in the female.

Many Orthoptera have a swollen oesophagus or crop followed by a gizzard with horny teeth. The salivary glands are large and usually provided with receptacles. The malpighian tubules are numerous. The ventral nerve-ganglia have undergone little fusion, there being three thoracic, and as many as seven abdominal, ganglia.

The sound-producing organs are in many cases confined to the male and their action is thought to attract the female. The latter lays comparatively few eggs and these are deposited either singly or in numbers in a case or capsule. The egg is supplied with an unusually large amount of food-yolk. The young hatch out in a condition closely resembling their parents, but

in no case do they have wings. These organs appear later and increase in size with each successive moult.

Sub-Order 1. CURSORIA.

Hind-legs differing but little from the others. This sub-order consists of five very divergent families with no intermediate forms.

Fam. 1. **Forficulidae**.* The earwigs have short tegmina: the second pair of wings are first folded like a fan, and then folded into four like a piece of note-paper. The cerci have the form of stout forceps which assist in folding the wings, and arise from an eleventh abdominal segment in the embryo. Wingless forms are frequent. The genital orifice is double in the males of some species. In *Forficula* † L. (Fig. 418) the first abdominal tergum tends to fuse with the thorax; there is a similar but much more complete fusion in the Hymenoptera. *F. auricularia* L. (British) is the common earwig; it is largely carnivorous, eating insects and snails,

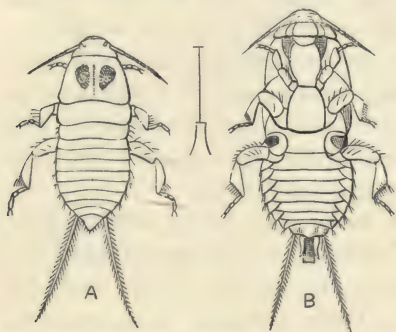


FIG. 419.—*Hemimerus talpoides*. Africa. (After de Saussure). A upper, B under surface.

and probably the injury it does to plants has been exaggerated, though it undoubtedly disfigures many flowers by nibbling the petals. The female guards her eggs but takes no interest in the young when they are hatched. *Chelidura pubescens*, also British, is apterous. Traces of tegmina appear in *Anisolabis* Fieber, of which genus *A. maritima* and *A. annulipes* are British. *Anechura* Scudd.; *Labidura* Leach, *L. riparia* is British; *Labia* Leach, a genus often seen in flight; *L. minor* is British, as

also *Apterygida albipennis* and *A. arachidis*. *Psalis* Serv. is the largest form.

Fam. 2. **Hemimeridae**.† A small family of blind and wingless Insects whose young develop in an extraordinary manner within the body of the mother. The cerci are long and flexible, not jointed. The few species known are external parasites on small mammals. *Hemimerus hanseni* is West African, living on the body of *Cricetomys*, a small rodent. The mouth-parts are remarkable, and include a pair of structures, one on either side of the hypopharynx, considered to be reduced maxillulae.

Fam. 3. **Blattidae**.§ Head bent down and in this position invisible from above, body oval and flattened. Coxae large, free, covering sterna of thorax. Tegmina variable in form or absent. Running Insects, with

* This family is regarded by some entomologists as an Order and named by some the Dermaptera and by others the Euplexoptera.

† *Das Thierreich*, 11 Lieferung, Forficulidae and Hemimeridae, de Bormans and Krauss, 1900; and British Orthoptera, *Naturalist Journal and Guide*, Huddersfield, 1897, M. Burr.

‡ H. de Saussure, *Spic. Ent. Genev.*, i, 1879; also H. J. Hansen, *Ent. Tidskr.*, xv, 1894, p. 65.

§ R. Shelford, *Trans. Ent. Soc.*, London, 1906, p. 231.

the three pairs of legs similar. This family includes the cockroaches, often incorrectly called "black-beetles." A few species have become domesticated, but they are inadequate to give any idea of the number, variety and beauty of the group in nature. The antennae are very long and both they and the palps are active in testing the nature of the ground on which the insect finds itself. The pronotum is large and overhangs the head. The abdomen is broad and its posterior segments are invisible, being tucked into those which precede them. In the chamber thus formed the egg-capsule is moulded and carried about by the female until she finds a convenient place in which to deposit it. Both sexes bear cerci and the males in addition are provided with anal styles. The wings are often large in *Anaplecta*, with a distal portion devoid of nervures; in *Diploptera* there is a special distal area on which occur nervures, but they are unrelated with those of the basal portion. Internally the gut-like chylific ventricle, which bears at its line of junction with the gizzard eight caeca, is worthy of notice. Some genera, e.g. *Panchlora*, are viviparous. The food of cockroaches is nominally dead animal matter, but the domesticated species enjoy a very mixed diet, and on ship-board make themselves a nuisance at night by nibbling one's nails. They are valued in some quarters since they are said to devour bed-bugs. They apparently live several years, and some species of *Periplaneta* only become adult after their seventh moult, which takes place in the fourth year. Their remains show that they were common in the Carboniferous epoch.

The Blattidae are divided into the following sub-families,* the representative genera of which may be mentioned:—

1. **Ectobiinae.** *Ectobia* Westw. et auct.; *E. lapponica*, *E. panzeri* and *E. livida* are British; *Plectoptera* Sauss.; *Hemipterota* Sauss.; *Anaptycta* Br.; *Chorisoneura* Br.; *Anaplecta* Burm.; *Theganopteryx* Brs.

2. **Phyllodromiinae.** The small cockroach *Phyllodromia* (*Blatta*) *germanica*, common in Eastern and Northern Europe and in the United States, has obtained a footing in this country. In America it is known as the "Croton bug."

3. **Nyctiborinae.** American. *Nyctibora* Burm.; *Megaloblatta* Dohrn.

4. **Epilamprinae.** *Notolampra* Sauss.; *Epilampra* Burm.

5. **Periplanetinae.** *Polyzosteria* Burm.; *Periplaneta* Burm., two species of which are common in Great Britain; *P. (Blatta) orientalis* the common cockroach of kitchens, and *P. americana* common on ships and in docks; this species sometimes migrates to fresh quarters in enormous hordes. These two species and *Phyllodromia germanica* are the three British cockroaches. *Atemeletra* Brun.; *Chalcolampra* Sauss.; *Deropeltis* Burm.; *Archiblatta* Snellen.

6. **Panchlorinae.** *Leucophaea* Br.; *Rhyparobia* Krauss; *Rh. maderae* is an introduced form in Britain; *Panchlora* Burm.

7. **Blaberinae.** American. *Blabera* Serv.; *B. gigantea* has been found in docks and wharves in Britain; *Blaptica* Stål; *Hemiblabea* Sauss.

8. **Corydinae.** In the male of the handsome genus *Corydia* Serv. and in *Heterogamia* the peculiar fenestrae seen on the head of *Periplaneta*, etc., are replaced by ocelli; *Homoeogamia* Burm.

* Brunner von Watterwyl, *Ann. Mus. Genova*, xxxiii, 1893, p. 5; and *Biol. Cent. Americana, Orthoptera*, vol. i, 1893-99.

9. **Oxyhaloinae.** *Hypnorma* has brightly coloured antennae and a median suture between the tegmina like that of a beetle; the head also is visible from above; *Diploptera* Sauss.; *Oxyhaloa* Br.

10. **Perisphaerinae.** *Gromphadorhina*, a wingless form from Madagascar with a stout body over three inches in length. *Pseudoglomeris*, whose name recalls its resemblance to the pill-millipede *Glomeris*.

11. **Panesthiinae.** *Panesthia* Serv.; *Plana* Br.; *Dasyposoma*; *Parahormetica*.

12. **Geoscaphaurinae**, a recent sub-family established for an extraordinary digging insect from Australia.

Fam. 4. **Mantidae.** Head bent down. Prothorax usually elongated and bearing a pair of large raptorial legs with free coxae, tarsi 5-jointed, with no pad (arolium) between the two claws. The second and third pair of legs simpler. Two-jointed anal styles.

The soothsayers or praying-insects have very mobile heads, so bent down in some species that the mouth points almost backwards. The second

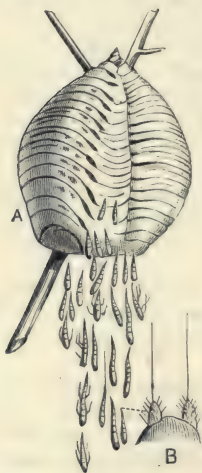


FIG. 420.—Egg-case of *Mantis* with young escaping. A the case with young in their position of suspension; B cerci of the young form magnified, showing the suspensory threads (after Brongniart).

maxillae have hardly fused to form a labium. The femur and tibia of the anterior legs are toothed, and the tibia shuts down into the femur with much the same action as that of the blade of a pocket knife shutting into the handle. With this the *Mantis* seizes its prey—for the most part small insects—gliding towards them with sluggish but stealthy movements. When at rest the front part of the body is raised, and the anterior legs are usually lifted in an attitude of prayer, which gives an innocent but entirely misleading appearance to the insect. In their chief features the wings are not unlike those of the *Blattidae*, but are perhaps more developed. Many of the *Mantidae* have a quiet inconspicuous appearance, but others show a remarkable resemblance to the structures on which they rest. Thus the Indian *Amorphoscelis annulicornis* mimics the bark of trees: *Eremiaphila*, which lives in deserts, is almost indistinguishable from the sandy soil; whilst the young of *Hymenopus bicornis* and *Gongylus gongyloides* simulate flowers of varying hue. *Harpax ocellata* is said to change colour like a chameleon. The number of species of *Mantidae* is put at about 600; they are largely tropical. Some dozen or more are met with in the Mediterranean area, and *Mantis*

religiosa occurs as far north as central France, but there are no British species. The eggs are laid in a peculiar ootheca formed by a foam-like fluid which exudes with the ova, and which as it hardens in the air is moulded by the tips of the fore-wings. *M. religiosa* lays in the autumn and the young forms emerge during the following June (Fig. 420). They then leave the ootheca but remain attached to it by a silken thread fastened to their cerci; only after their first moult do they become free.

The species are grouped in six sub-families:—

1. **Amorphoscelinae.** *Paraoxyptilus* Sauss.; *Discothera* Bon. and

Fin.; *Mantoidea* Newm. shows few of the well-marked features of the family.

2. **Orthoderinae.** *Pyrgomantis* Gerst., the female has rudimentary wings; *Eremiaphila* Lef., highly modified desert dwellers.

3. **Mantinae.** *Micromantis* Sauss.; *Odontomantis* Sauss.; *Hapalomantis* Stål; *Tropidomantis* Stål; *Archimantis* Sauss.; *Pseudomantis* Sauss.; *Mantis* L., *Callimantis* Stål.

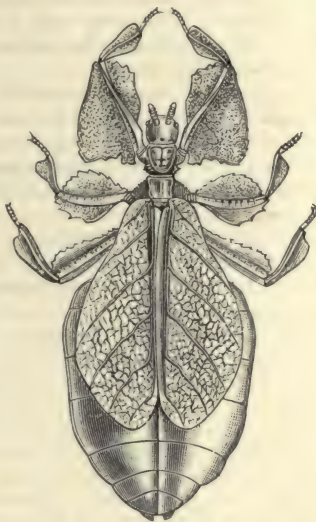
4. **Harpaginae.** *Harpax* Serv.; *Pseudoharpax* Sauss.

5. **Vatinae.** *Vates* Burm.; *Pseudovates* Sauss.; *Stenophylla* Westw.; *Stenovates* Sauss.

6. **Empusinae.** *Gongylus* Thunb.; *Empusa* Illig.; *Idolum* Sauss.

Fam. 5. **Phasmidae.*** Head protruded, prothorax short but mesothorax much elongated, the legs are similar one to another, cerci present but unjointed, tegmina small or, like the hind-wings, sometimes absent, sexes often unlike.

The *Phasmidae* are commonly known as leaf- or stick-insects and in them the mimicry of plant-structures reaches its highest development (Fig. 421). They are often large insects, attaining in some cases a length of nine inches. Usually the antennae are many jointed, the eyes prominent and supplemented by ocelli. The prothorax, in contrast to that of the *Mantidae*, is short even in the lengthy stick-insects; the mesothorax always big. The abdomen is usually elongate and of 9-10 segments, the cerci are flattened unjointed plates. The anterior legs are often stretched forward, the femora guarding and concealing each side of the head. The eggs maintain the tradition of the family as mimickers of vegetable organisms by resembling seeds, and like many seeds they are scattered promiscuously and not laid in oothecas. Many of the odd extensions of the integument characteristic of these insects are already visible when the young leave the egg, and they are exaggerated at each subsequent moult. The newly hatched young of the wingless forms closely resemble their parents. Other forms acquire wings after their second or third moult. As is so often the case in the Tracheata the females are much larger than the males, and the latter are more mobile and frequently possess wings even when the females are wingless; on the other hand, the mimicry of the females is far more perfect than is that of the males, who



× $\frac{2}{3}$

FIG. 421.—*Phyllium scythe*, female. Sylhet (after Westwood).

* Joly, *Mem. Ac. Sci. Toulouse* (7) iii, p. 1. Göldi, *Zool. Jahrb. Syst.* 1886, p. 724; also Brunner von Wattenwyl and Redtenbacher, *Die Insektenfamilie der Phasmiden*, Leipzig, in course of publication.

are less important in the perpetuation of the race. The anterior wings are usually those which most closely mimic leaves, but the legs and other parts of the body may also be flattened and leaf-like (Fig. 421). In the genus *Phyllium* this is carried so far that specimens nibble each other, apparently under the impression that they are eating leaves. The nervures of the tegmen are very peculiar and the hind-wings in the female are represented by rudiments. As the *Phyllium* ages its leaf-like wings are said to assume autumn tints. Other genera such as *Lonchodes*, *Bacillus*, etc., resemble twigs or grass-stalks; others again, such as *Ceroys*, bear many thorns or spines. All are vegetable eaters and at times are so numerous and so voracious as to be counted amongst the insect-pests. There are some 600 species, for the most part tropical or sub-tropical; the leaf-insect *Phyllium* has a predilection for islands. Four or five species occur in South Europe, but the whole family is very intolerant of cold. Australia is perhaps their present head-quarters.

There are twelve sub-families:—

1. Sub-fam. **Lonchodinae**. This sub-family is confined to the Old World. *Lonchodes* Gray; *Promachus* Stål.
2. Sub-fam. **Bacunculinae**, an American sub-family. *Phantasis* Sauss.; *Lamponius* Stål; *Bacunculus* Burm.
3. Sub-fam. **Bacterinae**. *Bacteria* Latr.; *Haplopus* Gray; *Bactridium* Sauss.
4. Sub-fam. **Necrosclinae**. *Necrosclia* Serv.
5. Sub-fam. **Clitumninae**. *Clitumnus* Stål.
6. Sub-fam. **Acerophyllinae**. *Tropidoderus* Gray.
7. Sub-fam. **Cladomorphinae**. *Cladomorphus* Gray.
8. Sub-fam. **Anisomorphinae**, an American sub-family. *Anisomorpha* Gray.
9. Sub-fam. **Phasminae**, with one exception *Orobia*, also an American sub-family. *Orobia* Stål; *Phasma* Stål; *Planudes* Stål.
10. Sub-fam. **Aschipasminae**. *Aschipasma* Westw.; *Perla* *morpha* Serv.
11. Sub-fam. **Bacillinae**. *Bacillus* Latr.; *Phalces* Stål.
12. Sub-fam. **Phyllinae**. *Phyllium* Illig.; *Chitoniscus* Stål.

Sub-order II. SALTATORIA.

Hind-legs lengthened and in most cases thickened for leaping; auditory and stridulating organs well developed.

Fam. 6. **Acridiidae**.* Antennae short with at most thirty segments; ovipositor short and not protruding from hind-end of female; tarsi with but three segments; auditory apparatus on first abdominal segment.

This family is the most numerous both as regards species and individuals of the Orthoptera. It comprises the common grasshoppers of our fields and the destructive locusts whose countless hosts destroy the vegetation of all the warmer regions of the earth. The head is large, bent downwards, and partly concealed by the prothorax; the eyes are large, and there are three ocelli. The short antennae offer a ready mark of differentiation from the Locustidae and Gryllidae. The prothorax is large, often crested and usually warty. The whole body is somewhat flattened from side to

* Bolivar., *Ann. Soc. Esp.*, xiii, 1884, p. 1. De Saussure, *Spicilegium entomologica Genevensis*, Pt. 2, 1887, and *Mem. Soc. Phys. Geneva*, xxviii, 1884. Brunner van Wattenwyl, *Bull. Soc. Rouen*, 1885.

side and the coxae of the legs are attached to the sides of the thorax, not to the ventral surface. Eight distinct segments can be counted in the abdomen and behind the last are the organs connected with reproduction. The tegmina are long and narrow; the hind-wings fold up like a fan and are covered by the tegmina. The hind legs are often very long and powerful and are used for jumping. The well-known noise made by grasshoppers is produced by rubbing a row of minute prominences on the inner surface of the femur of the last legs against certain projecting veins on the outer side of the tegmina. This sound-producing apparatus is better developed in the males than in the females, the last named sex rarely producing sounds audible to our ears. The auditory organs are one on either side of the first abdominal segment; each consists of a membrane surrounded by a complex rim and well supplied with nerves, muscles and tracheae. It is well developed in both sexes. This family is remarkable amongst the Orthoptera for possessing spacious vesicles connected with the tracheae, and when these are fully inflated they doubtless serve to lighten the body of the insect during its flights (Fig. 386). The female prepares by means of certain gonapophyses a hole in the earth in which she deposits her eggs and a quantity of a fluid which hardens around them. In this way *Caloptenus spretus* lays about 100 eggs, in four batches of about twenty-five. The young moult soon after leaving the egg and the last stage, the sixth, is the adult. During the post-embryonic development there is a considerable change of colour as well as an increase in the complexity of parts. The Acridiidae are vegetable eaters, and include most of those insects popularly known as "locusts" which at times do incalculable harm to the plant-world. When for some unknown reason species of this family increase at a prodigious rate, and above all when, as is the case with many species, they develop migratory habits, the vegetation of whole regions may be destroyed. During a single season in the island of Cyprus over 1,300 tons of "locust" egg-cases have been destroyed and this figure gives some slight idea of the gravity of the plague. The swarms do not necessarily occur every year, in fact there is as a rule some interval between each attack. The predisposing cause is unknown. One of the most important migratory species, *Pachytylus cinerascens* (Fig. 422), is indigenous to Belgium but gives rise to no swarms in that country. The direction of the locust flight seems to depend largely on the wind, and the insects are said to fly at great heights. The migratory instinct is not confined to the winged adult; the wingless young sometimes jump through the land in countless hordes clearing off every blade of grass as they progress, and doing perhaps more damage than the winged adults.

In the Old World, especially in the East, the most abundant "locust" is *Pachytylus cinerascens*, which when denuded of its wings and legs and fried in butter tastes

not unlike shrimps and is eaten by the inhabitants of Palestine. *P. migratorius* is rather more restricted in range, being limited to E. Europe



FIG. 422.—European migratory locust, *Pachytylus cinerascens* ♀. From Sharp.

and Turkestan. *P. migratorioides* is E. African. *P. marmoratus* is widely found in the warmer parts of the East, whilst *P. nigrofasciatus* spreads into colder regions. *Schistocerca peregrina* reaches from N. Africa to N.W. India and is probably the "locust" which plagued Pharaoh and his people. *S. americana* is migratory in the United States and several other species are American. The Rocky Mountain Locust is *Caloptenus spretus*.

The Acridiidae comprise the following nine sub-families:—

1. **Tettiginae.** In this large sub-family the pronotum is extended backwards as a hood or cover over the body, and this extension often takes a grotesque and bizarre form. A similar outgrowth occurs in the Membracidae, a sub-family of the Hemiptera. *Tettix bipunctatus* and *T. subulatus* are British. *Xerophyllum*; *Cladonotus*; *Scelimena*.

2. **Pneumorinae.** Large South African forms with few species. *Pneumora*.

3. **Mastacinae.** Rare and tropical. *Mastax*.

4. **Proscopiinae.** Wings small or absent. The insects frequently resemble Phasmids, but here it is the prothorax which is elongated. *Cephalocoema*.

5. **Pyrgomorphinae.** *Pyrgomorpha*.

6. **Tryxalinae.** A numerous sub-family. *Mecostethus grossus* is British; *Tryxalis*.

7. **Pamphaginae.** Chiefly African and Mediterranean. *Xiphocera*.

8. **Oedipodinae.** This sub-family includes most of the migratory locusts of the Old World. *Pachytylus*; *Methone*; *Cuculligera*; *Trachypetra*.

9. **Acridiinae.** Most British Orthoptera belong to this sub-family. *Stenobothrus* with six British species; *Gomphocerus* with three; *Acridium*; *Caloptenus*.

Fam. 7. **Locustidae.*** Long, slender antennae of more than thirty segments; elongated, flattened and sword-like ovipositor; tarsi with four segments; auditory organs on tibiae of first legs; wingless forms numerous.

The Locustidae † are as a rule more delicately formed insects than the Acridiidae, are destitute of the tracheal air-vesicles, and do not take such prolonged flights as true locusts. The term "grasshopper" is applied indiscriminately to certain members of both the families *Acridiidae* and *Locustidae*. The shrill music of the Locustidae is produced by rubbing a file-like ridge beneath the base of the left tegmen over a ridge on the upper surface of the right tegmen. This apparatus is usually confined to the male. The ovipositor is sometimes as long as the body, or longer, and is used in placing the eggs in the earth or in slits made in stems of plants. Most of the insects pass the winter in the egg, and hatching out in the spring, become adult in about ten weeks after casting the skin—which the young insects economically eat—some four or five times. The Locustidae are largely nocturnal; they frequent trees and live largely on leaves, but they are not bigoted vegetarians and some are said to be

* Dewitz, *Zeitschr. wiss. Zool.* xxv, 1875, p. 174. Riley, *Ann. Rep. Insects, Missouri*, vi, 1874, p. 159.

† The family name is unfortunate as "locusts" belong to the Acridiidae. Some authorities substitute the name Phasgonuridea.

entirely carnivorous, living for the most part on other insects. The tegmina of some genera, e.g. *Pterochroza*, closely mimic leaves especially faded ones, even carrying the mimicry so far as to imitate the markings caused by larvae which mine in the tissues of the leaf. Others seem to escape molestation by mimicking ants, and some resemble twigs.



FIG. 423.—Katydid, *Microcentrum retinerve*. N. America (after Riley).

The Locustidae are divided into fifteen sub-families :—

1. **Phaneropterinae.** *Phaneroptera falcata* and *Leptophyes punctatissima* are British. *Microcentrum* includes many of the North American "Katydids." *Myrmecophana* mimics ants.

2. **Meconeminae.** *Meconema varium* is British and lays eggs in galls of *Cynips*.

3. **Mecopodinae.** *Mecopoda* with a very highly developed phonetic apparatus.

4. **Prochilinae.** The phasmid-like species are confined to this sub-family, e.g. *Phasmodes* and *Prochilus*.

5. **Pseudophyllinae.** *Pterochroza* and to a less extent *Cyrtophyllus* mimic leaves.

6. **Conocephalinae.** *Copiophora* with curious head bearing an ornamental outgrowth. *Megalodon*. *Xiphidium dorsale* is British.

7. **Tympanophorinae.**

8. **Locustinae.** *Locusta* includes the British green-grasshopper *L. viridissima*.

9. **Saginae.** *Peringueyella*, an elongated South African genus.

10. **Decticinae.** *Decticus verrucivorus* rarely taken in Britain, as is also *Thamnotrizon cinereus* and three species of *Platyellis*.

11. **Callimeninae**, with phonetic organs in both sexes.

12. **Ephippigerinae.** This sub-family also has phonetic organs in both sexes. *Ephippigera* mimics parts of plants.

13. **Hetrodinae.**

14. **Gryllacrinae.** *Schizodactylus* a curious form with the wings produced into curled processes.

15. **Stenopelmatinae.** Largely a cave-dwelling sub-family, whose members have enormously long antennae and legs, and no wings or phonetic organs.

Fam. 8. **Gryllidae.** Elongate very slender antennae; hind legs adapted for jumping; often a long spear-like, cylindrical ovipositor (not in *Gryllotalpinae*); tegmina with inner and posterior part flat on the back, the outer part folded at right angles on to the side of the body; tarsi three-jointed with some exceptions; wingless forms common: cerci anales often long, unsegmented.

FIG. 424.—*Gryllus campestris* ♂

Both in the ovipositor and in the position of the auditory and phonetic organs the Gryllidae or Crickets come close to the Locustidae, the chief divergences between the families resting in the arrangements of the tegmina, the usual number of the tarsal joints and the development of the unjointed cerci anales. The shrill note of the Gryllidae is caused by the rapid vibration of the tegmina, "the edge of one acting on the file of the other." The hind wings are usually longer than the tegmina

and often than the body. In the abdomen the pleura are markedly large and the abdominal stigmata correspondingly conspicuous. Crickets have but little beauty of shape, colour or voice. They seldom leave the ground, though the tree-crickets climb on to plants; with the exception of the *Gryllotalpinæ* they are herbivorous, and are very cosmopolitan in their distribution.

The Gryllidae are divided into seven sub-families:—

1. **Tridactylinae.** This sub-family departs from the usual rule inasmuch as its antennae are short, of some ten joints, and there is no ovipositor. Their wings also differ from those of other Gryllidae, and they have no auditory organ on the legs. On the whole their affinities are doubtful. *Tridactylus* South European; *Rhipipteryx* South American.

2. **Gryllotalpinæ.** *Gryllotalpa* (mole-crickets) burrows underground by means of stout fore-legs, which by a shear-like action cut through roots, and thus causes some damage to crops. It is largely carnivorous. *G. vulgaris*, now becoming rare in England, lays 200–400 eggs over

FIG. 425.—*Gryllotalpa vulgaris*.

which the mother watches carefully. These hatch in a month and the female feeds the larvae until they undergo their first moult; on the other hand the male occasionally devours them. *Cylindrodes* is an Australian genus, very destructive to plants.

3. **Myrmecophilinae.** *Myrmecophila*.

4. **Gryllinae.** *Gryllus campestris* is the field cricket, *G. (Acheta)*

domesticus the "cricket on the hearth": the latter seems strangely devoted to the dwellings of man, and it is doubtful if it leads a truly wild life. The adult male alone chirps. *Platyblemmus*; *Nemobius sylvestris* is taken in the New Forest.

5. **Oecanthinae.** *Oecanthus* with distinct diurnal and nocturnal "songs." 6. **Trigonidiinae.** *Stenogryllus*. 7. **Eneopterinae.**

Order 7. PLECOPTERA * (PERLARIA).

Fair sized insects with anterior wings long and slender, posterior wings larger and folding like a fan, both pairs membranous with very numerous nervures; the coxae are small and separated laterally; larvae aquatic; metamorphosis slight.

The "stone-flies" are a very small order of inconspicuous

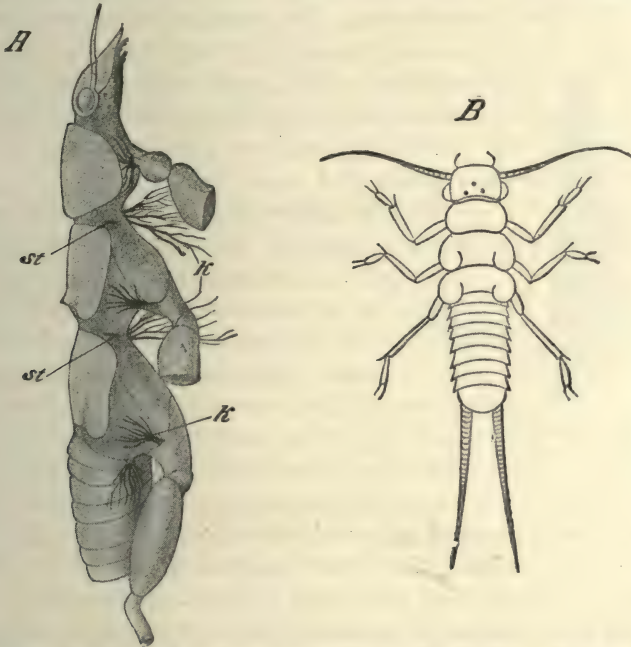


FIG. 426.—A. Perlid larva, lateral aspect (after Graber).; *k* gill-tufts; *st* stigmata; B. larva of *Perla bicaudata* (after Westwood).

insects, the described species of which hardly surpass two hundred in number. Their body is somewhat flattened. The head bears long, multi-segmented antennae, and as a rule somewhat

* Imhof, *Beitr. Anat. Perla maxima.*, Inaug. Dissert. Aarau, 1881. For British Species v. Cat. of Brit Neuroptera *Entom. Soc. London*, 1870.

feeble mouth parts, also two or three ocelli and moderately large compound eyes (Fig. 426). The thoracic segments are distinct, and, correlated with the gap between the bases of the legs, the sterna are well developed. The abdomen has ten distinct segments and often ends in a pair of long, jointed cerci. The legs are slender and have three tarsal segments. The tegmina lie flat on the back, one overlapping the other, and each bent down at the side so as to protect to some extent the sides of the body. In opposition to the usual rule the wings of the males are often reduced and smaller than those of the female.

The oesophagus is large and there is no distinct crop or proventriculus. The true stomach is small with ten lobes. The malpighian tubes are numerous. The nervous system comprises a small brain, three thoracic and six abdominal ganglia. Both male and female gonads form a ring like those of many Arachnida, and the latter bears a receptaculum on its course.



FIG. 427.—*Perla maxima*
(after Pictet).

The Plecoptera lay very numerous eggs, some thousands, each with a remarkable micropyle. The eggs are said to be carried about in a hollow on the ninth abdominal segment of the female before being deposited in the water. The larvae (Fig. 426) seem to prefer running streams and even torrents; and the adults, since they are not strong on the wing, usually frequent the vicinity of

such waters. The larvae are mostly found under stones; they have no stigmata and either absorb oxygen through the skin or through tuft-like gills plentifully supplied by tracheae. Such gills may persist until the imago instar is reached, and may coexist with functional stigmata, of which there are usually two pairs on the thorax and six on the abdomen. In the last aquatic or nymph stage the insect resembles the aerial adult, except in having no wings; but like the larva it is active and feeds on soft-bodied insects such as May-flies.

On the whole the Order is perhaps most closely connected with the Orthoptera and especially with the least specialized members of the family *Phasmidae*. It comprises but one family:—

Fam. 1. **Perlidae**. With the characters of the Order. There are a couple of dozen British representatives, and as the insects are unattractive and yet widely distributed it is probable that in all parts of the world many remain to be described. *Perla* British; *Pteronarcys*; *Isopteryx* with an auditory organ on the legs; *Dictyopteryx*; *Isogenus* British; *Nemoura*.

Order 8. PSOCOPTERA * (CORRODENTIA or PSOCIDAE).

Minute soft-bodied insects with hair-like antennae; wings absent or present and in the latter case the fore-wings are larger than the hind ones; prothorax small and in the winged species, hidden between head and mesothorax; tarsi with two or three segments; metamorphosis slight.

The numbers of existing and of described species is probably about equal to that of the Plecoptera, but there are rather more British species, some thirty or so. The antennae have from eleven to twenty-five segments. The mouth parts are well developed and the 1st maxilla bears a peculiar "pick." The thorax looks as if it had but two segments, since in the winged forms the prothorax is concealed, and in the wingless forms where it is apparent the meso- and meta-thorax are fused. The sterna are small and the coxae contiguous. The alimentary canal is simple, there is no crop or proventriculus, only four malpighian tubules, and a short intestine in *Clothilla*. The life-history of the group is not well known. The development of the wings varies much, but even when they are fully formed there seems a curious reluctance to use them; still at certain times clouds of small Psocids float on the wing. Ocelli usually occur in the winged forms and are absent in the apterous species. Probably the order comes nearer to the Termitidae than to any other.

Some Psocids have the wings covered with scales, which possess colours, and form patterns of extraordinary beauty and complexity, rivalling those of Microlepidoptera. Enderlein, who has devoted much study to the group and described many of these scaly-winged forms,† unites the Psocids with the Embiidæ,



FIG. 423.—*Psocus fasciatus*, England (after M'Lachlan).

* M'Lachlan, *Ent. Mon. Mag.*, iii. 1867, p. 177. Derham, *Phil. Trans.* xxii, 1701, and xxiv, 1704. Enderlein, *Zool. Anz.*, xxvi, 1903, p. 423.

† *Spolia Zeylanica*, vol. iv, Dec. 1906, pp. 39-122 and plates.

Termitidae, and Mallophaga in a single order Corrodentia, making the Psocids a special sub-order **Copeognatha*** The group is also of interest from the fact that very many members of it are preserved in amber. There is but one family :—

Fam. 1. **Psocidae**. With the characters of the Order. *Psocus*, many species of this genus live in colonies on the rough, lichen-covered bark of trees. They spin silken webs which cover the colony and lay their eggs in clusters which they protect with a coating of chewed woody fibre. *Thyrsophorus* from Brazil is the largest genus measuring an inch across the outstretched wings. *Embidopsocus* is said to show affinities with the Embiidae. *Clothilla* and according to others *Atropos* share, with the Beetle *Anobium*, the credit of being death-watches. Their tappings alarm the superstitious, though it is not absolutely proved that they cause the regularly repeated noise. Both the last named species are "book-lice," and by eating the starch paste employed in book-bindings and in lining insect cabinets, cause much annoyance to librarians and entomologists. If undisturbed they may exist in great swarms.

Order 9. ISOPTERA (TERMITIDAE).†

Social insects with or without wings ; when present all the wings lie flat on the back ; hind- and fore-wings are alike membranous and much longer than the body ; they are readily cast off, and breaking along a weakened line, leave a small projection behind ; the ten abdominal segments end in a pair of short cerci ; metamorphosis slight and gradual.

The termites are popularly known as white ants, a misleading



FIG. 429.—Male of *Termes lucifugus*.

name as they are not ants and by no means always white. The head is large and in some grades of their communities gigantic ; it may bear com-

compound eyes and at most two ocelli, but many termites are blind. The antennae have nine to thirty-one segments (Fig. 492).

The skin is usually thin even where the chitin is best developed,

* *Zool. Anz.*, vol. xxvi, 1903, p. 423.

† Grassi and Sandias, *Atti. Acc. Gioen.*, vi, 1893, and vii, 1894. Hagen *P. Boston, Soc.*, xx, 1878, p. 118. Lespes, *Ann. Sci. Nat. Zool.* (4), v, 1856, p. 227. Grassi, *Zool. Anz.*, xii, 1889, p. 360, and *Q.J.M.S.*, xxxix, 1896, p. 245.

and termites are emphatically soft insects. The abdomen is bulky and in the queens enormous. The members of the communities apparently communicate one with another by means of sound, and an auditory apparatus exists on the anterior tibia as in the Locustidae. The wings, which are used but for one flight and are then cast off, possess few but varying nervures, three chief longitudinal ones being present. Ten spiracles are described. Salivary glands and receptacles are present and large; a crop is found, but not always a proventriculus. Behind the insertion of the few (4-8) malpighian tubules is a large swelling, the "paunch," which is succeeded by the small intestine. Three thoracic and six abdominal ganglia are described. The testes and ovaries are simple and vary in size in different species and specimens.

It is not yet possible to give a generalized account of the social communities of the termites, partly because our knowledge is still very incomplete, and partly because the organization of the societies differ very greatly in different species. The classical example is the African *T. bellicosus* * which builds huge clay nests "comparable to human dwellings; some of them being twenty feet in height." From these nests extend a ramification of covered passages, for, except during the swarming-flight, the termites spend their life in the dark. Within the nest is a countless crowd of termites, and the whole of this community has been derived from a single royal couple which alone are capable of reproducing. It is thought that if the royal pair be destroyed the community perishes and if this be the case there can be no provision such as exists in other colonial Insects for repairing so grave a disaster. The queen attains enormous proportions; by the enlargement of the ovarian tubes her abdomen swells to such an extent that she becomes from twenty to thirty thousand times the normal size. She ceaselessly lays eggs which are carried away and tended by the workers. Owing to her bulk it is quite impossible for her to leave the royal cell to which her mate is also confined. The growth which is here described is probably a unique case, since Insects as a rule never grow after reaching the adult instar.

Besides the (i) king and queen we find in the colony enormous

* Smeathman, *Phil. Trans.*, lxxi, 1781, p. 139; and Savage, *Ann. Mag. Nat. Hist.* (2), v, 1850, p. 92.

numbers of (ii) workers, and (iii) soldiers. These are male and female with sexual organs arrested in development and without wings. The soldiers are distinguished from the workers by their size rather than by their valour; in fact the workers are the chief fighters. In *T. bellicosus* the soldier is fifteen times the size of the worker. The head is enormous and the mandibles are especially enlarged and show well-marked specific characters. A certain modification, in which the head is prolonged into a snout, from which issues a fluid used in cementing the walls of the nest, gives origin to a sub-grade of soldiers called the *nasuti*. Besides the forms already mentioned the nest is crowded with larvae, which leave the egg in an active but soft and blind condition. These young are at first all alike, some of them are destined to form workers and soldiers, others to acquire wings and to leave the nest in countless swarms. The latter probably pair in their flight and dropping to the earth shake off their wings. Should a male and female alight together they may succeed in founding a new colony, retaining in them a sufficient store of nutriment to last till the first batch of workers hatches out; these then begin to tend their royal parents.

T. lucifugus is found in the south of Europe and in the United States. Its galleries mostly lead to wood of various kinds, old trees, parts of buildings and even furniture. There are workers and soldiers and larvae in various stages but apparently no royal pair. The reproductive functions have been taken on by a number of complemental females, which have not completed the normal cycle of development and in externals resemble one or other of the late larval stages, for in this species the reproductive organs may become active at differing stages of development. Kings are not always to be found, and it may be that in the case of the male the reign is transitory and that the kings die or are killed as soon as they have fertilized the females. The development of the community takes eighteen to twenty-three months, during which several swarms of winged individuals are given off: most of these fall victims to insectivorous birds, etc., but some pairs escape and seek to establish new colonies, in which case the female would be a true queen whose functions are later assumed by the complemental females.

Calotermes flavicollis is the second species of European termite. It inhabits the Mediterranean region. It has no specialized

worker grade and the affairs of the community are carried on by the soldiers and active larvae. This species lives in passages, excavated in dead or decaying trees; they build up barriers with their own ejecta and line the galleries with secretions from their salivary glands or from the anterior end of the alimentary canal. The colony is small, with some hundreds of individuals, but rarely numbering a thousand. The royal couple move about and their progeny increases slowly; two years may see a family of fifty, and when some five hundred have been produced the queen diminishes the output. The winged insects take more than a year before they swarm, after which they pair off and start new colonies.

From what has been said it is evident that the continuation of a colony of termites depends on the well-being of the king and queen or of a small number of queens. To diminish the risk which is concentrated on a few individuals, the termites manage to keep certain of the larval forms (Fig. 430) in such a condition that should anything happen to the royal pair, they may by proper attention—probably a change of diet—become reproductively active. The activity of the reproductive functions takes place in an insect still in a larval stage.* Before it sets in these individuals are known as “reserve” or “complementary” kings and queens; after it has been brought into use they are known as “substitution” royalties. In the case of *T. lucifugus* the colony is mainly carried on by such forms. The reserve or complementary monarchs are however not derived from stages immediately preceding the final or normal adult instar, but from some earlier larval stage, and by no means always from insects in the same instar.

The termites, inhabiting their enormous nests, keep the interior of their dwelling scrupulously clean. They not only eat

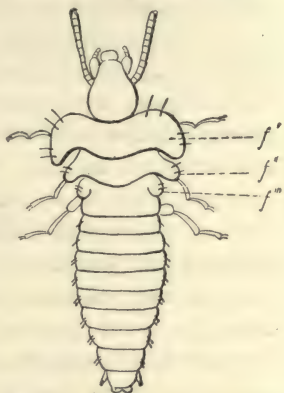


FIG. 430.—Larvae of *Caloterme rugosus* (after F. Müller). *f'* wing-like appendages of the prothorax; *f''* rudiment of the fore-wing; *f'''* rudiment of the hind-wing.

* Cf. *Amblystoma*. The larval stages with active reproductive powers are sometimes called “neotenic.”

all refuse including what has passed through the alimentary canals of others, and hence termed proctodaeal food, but the cast skins and the dead bodies of their companions. When the last trace of nutriment has been absorbed from the repeatedly digested food, the ejecta are either left outside the nest, or carried outside, or used in plastering the walls of the galleries. Another kind of food is the regurgitated contents of the crop called stomodaeal food, and a third is the secretion of the salivary glands, whilst the soldiers at any rate consume alive the bodies of any fellow *Calotermes* which may be ill or disabled. They occasionally kill but do not eat members of other species such as *T. lucifugus*. The young are at first nourished by the salivary secretion alone, later they take stomodaeal and proctodaeal food and at length are able to support a diet of triturated wood.

Since as far as we know termites of all grades resemble one another when first hatched; and since it is evident that the grade of the insect can be determined by the community, for not only can substitution royalties be produced, but forms far along the road leading to the winged state can be diverted and turned into soldiers, their rudimentary wings being absorbed; it seems evident that heredity cannot be the determining cause of any individual assuming its final grade. Grassi, whose researches have done much to throw light upon the problems of termite life, attributes the various forms we know to diet, and it is probable that he is right.

Termites flourish best in the tropics and subtropics, but a few, as we have seen, spread into the warmer temperate regions. Their nests are made of chewed wood or earth solidified by the excretions of the insect. The earth which forms their galleries is often carried in the form of branching tunnels even on to the finer twigs of the trees they are devouring; and as these galleries crumble from time to time the soil returns to the surface, and it has been suggested that in Africa termites take the place of earthworms in renewing the surface soil. An Australian species has the peculiarity of placing its flattened upright nest with the long axis pointing east and west. In the nests of *T. bellicosus* and *T. augustatus* the nurseries, where the young are reared, are lined with the mycelium of a fungus. The habit which compels a termite to work in the dark, under cover of some excavated tunnel or hastily constructed gallery, is thought to be connected

with the fact that they require a certain amount of heat and moisture. When removed from their retreats to the outer air, except during the swarming flight, they soon die.

There is a single family :—

Fam. 1. **Termitidae.** With the characters of the Order. There are about one hundred described species, but it is thought that many await description and that there may be some thousand in all. *Termes* has representatives in all the warmer parts of the globe, often very destructive in their habits. The woodwork of the Imperial greenhouses at Schönbrunn, Vienna, was completely eaten away a few years ago by *T. flavipes*, a species which in both worlds attains a high northern limit for a termite. *Eutermes*, with several American species, often inhabits the nests of *Anoplotermes*, a form in which the soldier grade does not develop. *Hodotermes* * is thought to produce no winged forms; it is at any rate in some species a harvesting form, collecting both grass and leaves. *Calotermes* has already been described.

Order 10. EMBIOPTERA † (EMBIIDAE).

Small insects with rather drawn-out bodies; pro-thorax small, but meso- and meta-thorax elongate; with four similar wings or none; three or four longitudinal and a few transverse nervures. Not social.

This is a very small order with some twenty described species. They inhabit warm climates, are unattractive, and have received little attention. The antennae have from fifteen to twenty-four segments. The coxae are separate, the tarsi three-segmented, the abdomen has ten segments and carries a pair of two-segmented cerci. The proximal segment of the anterior tarsus gives exit to the secretion of a gland which hardens into silk, with which tunnel-like webs are woven under stones, where the insects live in a warm, moist atmosphere. Their food is vegetable.

There is but one family :—

Fam. 1. **Embiidae.** With the characters of the Order. *Oligotoma* is Indian and Pacific and has been introduced into England. *Embia* Mediterranean.

Order 11. EPHEMEROPTERA † (EPHEMERIDAE).

Fragile insects with poorly developed mouth-parts, the imago

* *P. Boston Soc.*, xi, 1868, p. 399.

† Hazen, *Canadian Entomologist*, xvii, 1885, Grassi, *Acc. Gioen*, vii, 1889.

‡ Pictet, *Hist. Nat. Neuropt.*, Ephémérines, 1843. Lubbock, *Tr. Linn. Soc. Zool.* xxiv, p. 61. Vaysière, *Ann. Sci. Nat. Zool.* (7), ix, 1890, p. 19. Ronalds, *Fly-Fisher's Entomology*, 4th ed., 1849. Eaton, Monograph of the May Flies, *Trans. Linn. Soc.* (2), iii, p. 1, 1888.

taking no food ; short antennae ; four membranous, closely reticulated wings, the hinder pair being much smaller than the fore-wings and at times absent ; the end of the abdomen bears three or two very long cerci ; larvae aquatic ; an active winged sub-imago stage precedes the imago.

These delicate insects known as May-flies spend almost all their life in a larval state, assuming their final stage but for a few hours and only for the purposes of reproduction. In the adult the mouth and its appendages have atrophied. The antennae are short and with but few segments. The eyes are

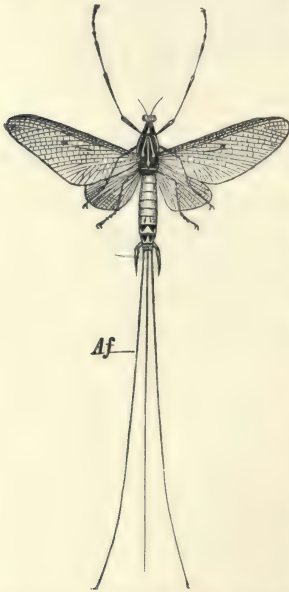


FIG. 431.—*Ephemera vulgata*. Af anal filaments.

large and complex, especially in the male, sometimes divided into two separate organs on each side, so that together with the three ocelli there are seven visual organs. The mesothorax, in correlation with the large fore-wings, is very bulky. The anterior legs are as a rule longer than the others, in some males very long. The abdomen has ten segments. The alimentary canal of the imago is very capacious and has thin, extensile walls : within it is stored air, the amount of which can apparently be controlled by the insect, and thus it acts as a balloon. The reproductive organs are the most primitive known amongst insects. Both male and female ducts are paired and devoid of accessory glands or diverticula ; they open

on the seventh abdominal sternite. The short life of the adult May-fly, often only a few hours, is spent in an aerial dance, during which the males fertilize the females, which then resort to the water to lay their eggs. Some in a fever of hurry deposit the contents of their ovaries in one mass which disintegrates into eggs as it sinks through the water, others more leisurely wash the extruded eggs from their abdomen by occasional dips in the stream or even creep below the water and deposit them under stones. The eggs are very numerous and may take half a year to hatch.

The larvae differ remarkably from the adults and are more peculiarly adapted to an aquatic existence than are those of any other Insects. The form which issues from the egg seems to be but little developed ; the number of moults is large, more than twenty in *Cloëon*, and each results in some change of form. At first the larvae show no respiratory organs, but after a few moults plate-like gills traversed by tracheae arise from the upper angles of

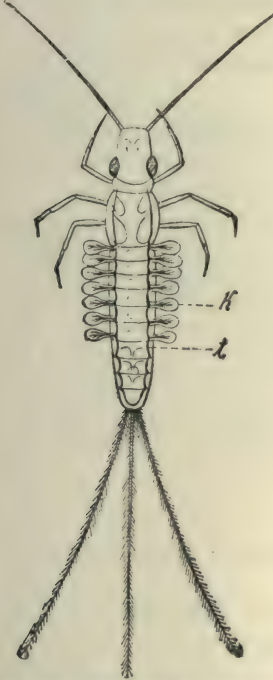


FIG. 432.—Ephemerid larva. *k* tracheal gills ; *t* principal trunks of the tracheal system.

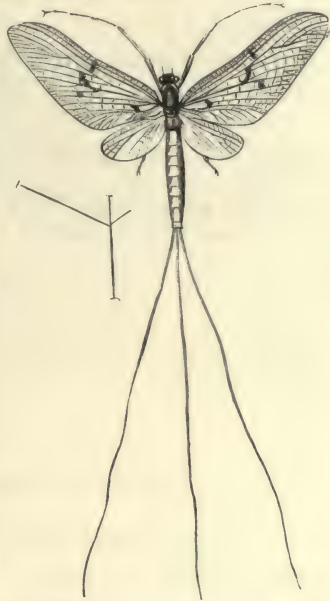


FIG. 433.—*Ephemera danica*, male, Britain. From Sharp.

the abdominal segments. The larvae may either dig or burrow in the banks and are then thought to eat mud ; or they may live on stones, in which case they are flattened and are carnivorous ; or they may swim freely about, or they may inhabit still waters, in which case they cover themselves with mud (Fig. 432). The later stages, when the wings begin to appear, are termed the nymphs, and these vary greatly as regards the arrangement of their tracheal gills. The tracheae are closed except momentarily at the time of ecdysis. The caudal appendages seem

also to take part in respiration, since each is supplied from the heart with a vessel which takes blood to the tip. The blood then returns to the abdomen, where it enters the general body-cavity and makes its way to the heart. Rectal respiration also occurs. When ready to give rise to the winged insect the nymph floats on the water, the skin splits and in a few seconds the winged creature has stepped out and flown away. This instar, though active and winged, is not the imago but is termed the subimago: it casts a last skin and the true imago emerges to live at most a few days, but oftener only for an hour or two, sometimes but for a few minutes.

May-flies, which if circumstances are favourable are born in countless numbers, are a favourite food of fishes, and form the "duns" "spinners" and "drakes" of the fly-fisher.

There is but one family:—

Fam. 1. **Ephemeridae**. With the characters of the Order. There are some two to three hundred species described, of which about forty are British; but the order is little known, and many more probably exist, though from the number and variety of the fossil forms it seems that the group is a disappearing one. *Ephemera* (Fig. 433) and *Cloëon* are common British genera. *Prosopistoma* is interesting, as it was long taken to be a crustacean from the pro- and meso-thorax forming a gill-chamber concealing five pairs of tracheal gills, like a Decapod. It is European and African.

Order 12. PARANEUROPTERA * (ODONATA : LIBELLULIDAE).

Long, slender insects with mobile heads, large eyes and short antennae ending in bristles; four transparent wings similar in appearance and size, arising behind the level of the legs, with many nervures; larvae aquatic.

Dragon-flies are easily recognized. The head is large and a great part of its surface is usually occupied by the enormous compound eyes, besides which there are three ocelli. The mouth parts are adapted for catching insects, which the dragon-fly does on the wing. The upper lip is large, the maxillae are toothed with a palp of one segment, the labium is wide and chiefly built up of the palps, the mandibles are powerful. The

* Calvert, *Trans. Amer. ent. Soc.*, xx, 1893, p. 159. Evans, *British Libellulinae*, 1845. Hagen, *Ent. Annual*, 1857. M'Lachlan, *Cat. Brit. Neuropt.* 1857, and *Ent. Mon. Mag.*, xx, 1854, p. 251.

prothorax is small; the meso- and meta-thorax are combined, and have their ventral portions pushed forward carrying the insertion of the legs with them; in the extreme cases the mesothorax lies very largely above the meta-thorax. The abdomen is long and cylindrical, consisting of ten segments and ending in a pair of forceps-like processes (Fig. 434). Certain structures on the second abdominal segment in the male



FIG. 434.—*Anax formosus*. Britain (after Migneaux). (The legs are not in a natural position.)

serve as vesiculae seminales, though how the semen is conveyed to them from the opening of the common vas deferens on the ninth segment is not clear. It is from the second segment however that the female takes up the semen during the nuptial flight. The ova are placed in the water or on some aquatic plant. The larvae are characteristic. They undergo many moults, and after the first three or four, traces of wings are apparent. The labium of the nymph is very large and jointed like a carriage-step; it is sometimes called the mask. It

can be shot out with extreme rapidity to catch insect prey (Fig. 435). The alimentary canal in these instars is richly supplied with tracheae and respiratory water is pumped in and out *per*



FIG. 435.—*Aeschna* larva with rudimentary wings and mask.

anum, the action being at times with such force as to propel the nymphs forward. When there is no air in the water the tail is protruded from the surface and air is taken in by the anus in the place of water.

Dragon-flies sometimes migrate in large numbers, especially the genus *Libellula*. As a rule they frequent places such as country-lanes, hedges, and the banks of streams, where they are most likely to meet other insects, which they devour in large numbers, catching them on the wing, and apparently entangling them in their legs and then handing them on to the jaws. The larvae and nymphs are also very destructive not only to other insect larvae but to the fry of freshwater fish. They have no sting and are quite harmless when caught, although there are many legends to the contrary. There are some 2,000 species described and 46 of these are British. The order is divided into two families and seven sub-families :—

Fam. 1. **Anisopteridae.** Front and hind wings dissimilar, wings when at rest horizontal, eyes not pedunculated.

Sub-fam. 1. **Gomphinae.** Eyes wide apart. *Gomphus* brilliantly coloured: a primitive group.

Sub-fam. 2. **Cordulegasterinae.** Eyes touching at one point only. *Cordulegaster*; the imago have a regular "beat" when on the wing; the nymphs burrow in mud.

Sub-fam. 3. **Aeschninae.** Eyes in contact for some distance. A large group both in size and number. *Anax*; *Aeschna*; *Epieaeschna*.

Sub-fam. 4. **Corduliinae.** Eyes with a tubercle behind them.

Sub-fam. 5. **Libellulinae.** No tubercle behind eyes. Abdomen often prismatic in cross section. *Libellula*.

Fam. 2. **Xygoteridae.** Wings alike, when at rest vertical, eyes pedunculated. Damoiselle- or Damsel-flies.

Sub-fam. 1. **Calepteryginae.** Wings with at least 5 cross nervures between the 1st and 2nd longitudinal nervures. A primitive group. *Calepteryx* haunts woods. *Hetaerina*; *Palaeophlebia* Japan, has Calepterine wings and a Gomphine body; *Euphaea*.

Sub-fam. 2. **Agriioninae.** Wings with only 2 cross nervures between the 1st and 2nd longitudinal nervures. Often small and very delicate insects. *Agriion*; *Lestes*; *Enallagma*; the tropical species *Mecistogaster* and *Megaloprepus* exceed in length of body and stretch of wing all other insects.

Order 13. THYSANOPTERA * (PHYSOPODA).

Small insects ; the mandibles are reduced to stylets and the mouth-parts are bent back under the prothorax ; wings either four, long, narrow and fringed with hairs, or absent ; tarsi of 1 or 2 segments. Young resemble adults, but there is a pupal instar.

The usually minute insects, known as *Thrips*, which constitute this order, are as to their mouth parts somewhat intermediate between the preceding orders and the Hemiptera. As in the last named order these appendages are folded back against the prothorax and the mandibles are reduced to piercing stylets or a single stylet—for the right mandible seems to be suppressed—concealed in a beak composed of the upper lip and maxillae. Both 1st and 2nd maxillae retain their palps. The antennae are 6-9 segmented. Three ocelli are present in the winged species but absent in the apterous forms. The abdomen has ten segments with stigmata on the 2nd and 8th segments ; the remaining two stigmata are meso- and meta-thoracic. Four malpighian tubes are present. The larvae resemble in form the adults, and eat the same food. Wings begin to appear after the third moult, but the instar preceding the adult is usually motionless and takes no food. The feet have a curious bladder capable of being distended ; it protrudes between the two terminal claws.

Thrips are said to suck the juices of plants, and undoubtedly some, e.g. the Corn-thrips in Europe and the Onion-thrips in America, do much damage ; other observers think they live on pollen, etc. They are usually found amongst the flowers of plants and are common in green-houses. Some live under bark, some amongst fungi and some cause the formation of vegetable galls which they inhabit. Parthenogenesis occurs.

The order comprises some 135 species of which 117 are European and some 50 British, but as the insects are small many more probably remain to be described. It comprises three families :—

Fam. 1. **Aeolothripidae.** Antennae with 9 segments ; fore-wings with a few nervures ; an ovipositor of four processes arises from the 8th and 9th segments of the abdomen and when extended is bent backwards. Three pairs of stigmata. *Aeolothrips*.

Fam. 2. **Thripidae.** This family agrees with the preceding in the

* Uzel., *Monog. d. Ordnung Thysanopterc*, Königgrätz, 1895. Halliday, *Ent. Mag.*, iii, 1836, p. 439, and iv, 1837, p. 144.

number of its stigmata and in its wing nervures, but its ovipositor is curved downwards and not backwards, and its antennae have 8 segments. *Thrips*, *Limothrips*.

These two families are sometimes known as the Terebrantia.

Fam. 3. **Phloeothripidae**. No wing nervures or at most one longitudinal one; antennae with 8 segments; body flat and last abdominal segment tubular. *Phloeothrips*; *Anthothrips*.

This family is sometimes known as the Tubulifera.

Order 14. HEMIPTERA * (RHYNCHOTA).

Mouth parts form a jointed beak or proboscis bent backwards under the thorax; wings with rare exceptions four, the anterior pair either half horny and half membranous, in repose lying flat on the back (Heteroptera), or of the same consistency throughout and sloping over the abdomen (Homoptera). Little metamorphosis.

A very variable and very large order, which includes bugs, plant-lice, scale-insects, etc. Some 20,000 species are already known, of which about two-thirds are Heteroptera. The mouth-parts are the truest mark of a Hemipteron, and their form is constant in the two great sub-orders Homoptera and Heteroptera, though these insects differ profoundly in other respects. The mouth-parts consist firstly of a tubular or rather grooved process formed from the labium; this may consist of one, two, three or four segments and is, when at rest, bent back under the thorax. It is devoid of palps and probably represents only the 2nd maxillae. The proximal portion of the groove is covered by a triangular labrum, but this does not extend far along the groove. If it be raised the remaining mouth parts can be seen lying in the groove. These consist of four chitinous setae capable of being protruded beyond the end of the groove, and they form the piercing organs of the insect. The outer stylets are usually regarded as representing the mandibles and the inner the 1st maxillae which like the 2nd are without palps. This view however is combated by some authorities. The stylets undoubtedly act as piercing organs, and the juices of animals or plants ascend the tube perhaps by capillarity or by the action of a sucking pharynx (Fig. 375).

The head varies greatly in shape and in some families is quite

* Schiödte, *Ann. Nat. Hist.* (4), vi, 1870, p. 225. Ashmead, *Entom. Americana*, iv, 1888. Saunders, *Hemiptera Heteroptera of the British Isles*, 1892. Pascoe, *Ann. Nat. Hist.* (5), ix, 1882, p. 424. Stål, *Hemiptera Africana*, 1866. Edwards, *Hemiptera Homoptera of the British Islands*, 1896.

monstrously swollen. Ocelli are often present. The antennae are small with 3-25 segments. The prothorax is large, in some cases monstrous, and free. The meta- and meso-thorax are well developed. The tarsi usually have three segments. The abdomen usually consists of 9, 10, or 11 segments. Its margins are often produced into a kind of shelf which enhances the flat appearance of many bugs. In Coccidae the number of segments is reduced. There are 3 thoracic and 7 abdominal stigmata in the *Heteroptera*. In many cases the female is provided with an ovipositor consisting of processes from the 8th and 9th segments.

Salivary glands are present, and also, in some cases at least, a special organ or syringe for forcing out the secretion which almost certainly sets up the irritation which ensues on a bite. There is a fine oesophagus and a crop but no gizzard. The number of malpighian tubules is small, usually four; but the Coccidae have only one pair and the Aphidae none at all. The nerve ganglia are few, the infra-oesophageal may be widely separated from the supra-oesophageal ganglion and may even fuse with the thoracic nerve mass.

The characteristic odour of bugs is due to the secretions of certain stink-glands which in the young open on to the upper surface of the abdomen and in the adults open on each side of the meta-sternum.

In many of the larger forms of Hemiptera the young hatch out very like their parents, but minus the wings. In the Homoptera however there is a more or less marked metamorphosis which reaches its fullest development in the Coccidae. Even in the Heteroptera there is usually a considerable change of colour and often of form between the young and old, and the change between the final or adult form and the preceding instar is often abrupt.

The order as a whole is injurious to human activity. A few destroy other harmful insects, but in the opinion of a well known authority "if anything were to exterminate the enemies of Hemiptera, we ourselves should probably be starved in the course of a few months."

Sub-order 1. **HETEROPTERA.**

Wings partly horny, partly membranous; anterior part of head not touching the coxae; the scutellum of the mesonotum is large.

There are about 430 British species of this sub-order.

Series A. **Gymnocerata**. *The antennae are conspicuous and easily moved.* This series includes all the terrestrial Heteroptera and the families *Hebridae* and *Hydrometridae* which seem to be becoming aquatic, as they frequent damp places or live on the surface of water.

Fam. 1. **Pentatomidae**. Shield-bugs. Scutellum very large, extending over the anterior half of abdomen and sometimes further. Antennae usually 5-segmented. Proboscis sheath 4-segmented. This is the largest family of the sub-order and includes some 4,000 species, characterized by great variety of form, brilliancy of colour and frequently by a distinctive odour. *Acanthosoma*, a British form, shows great maternal care for its eggs, which in this family are usually laid in clusters. The Pentatomids live largely on plant-juices and may, e.g. *Murgantia*, prove pests. Some however prey upon other insects, especially softer kinds.

Fam. 2. **Coreidae**. Scutellum does not reach the middle of abdomen. Proboscis-sheath 4-segmented. Antennae usually long and 4-segmented. Femora not knobbed. A large and widely distributed family; usually sad-coloured and at times with curious outgrowths from the sides of the body and from the hind-legs (*Leptoglossus*, *Diactor*). The members of this family live on plant-juices and may be destructive, e.g. the squash-bug *Anasa tristis*. *Phyllomorpha* carries its eggs on its back.

Fam. 3. **Berytidae**. Slender insects with the first segment of the antennae and the femora knobbed. A small family frequenting plants. *Jalysus*.

Fam. 4. **Lygaeidae**. Separated from the Coreidae by the upper surface of the head being arched and the insertion of the 4-segmented antennae being thrown ventralwards. Ocelli present. A large family of small, and as a rule inconspicuous, bugs. They suck the juices of plants and are often destructive, e.g. the chinch-bug *Blissus leucopterus* and the false chinch-bug *Nysius augustatus*. The former is said to cause an average annual loss in the United States of over £4,000,000.

Fam. 5. **Pyrrhocoridae**. The insects of this family closely resemble the Lygaeidae but have no ocelli. *Pyrrhocoris apterus*, a British form, is a good example of the dimorphism of the wings common in this and the preceding family. *Dysdercus suturellus* is the Cotton-stainer of the Southern States.

Fam. 6. **Tingidae**. Two tarsal segments, the preceding families having three. There is a curious net-like reticulation of the elytra and upper surface of body. Antennae knobbed. Front coxae extending to posterior end of thorax. A restricted family known as Lace-bugs; they are small and plant feeders, and survive the winter in the imago instar. *Copium*, *Gargaphia*, *Corythuca*.

Fam. 7. **Aradidae**. Flat and broad, scutellum pronounced. Abdomen projects beyond folded wings. Front coxae arise midway along prosternum. Small bizarre bugs living under bark and sucking the juices of fungi. *Aradus*, *Neuroctenus*.

Fam. 8. **Hebridae**. Minute; the under surface of the abdomen bears a velvety pile of short hairs. Antennae 5-segmented. Semi-aquatic, frequenting bog-moss, pond weeds and other damp plants. *Hebrus*, the only genus.

Fam. 9. **Hydrometridae**. Antennae 4-segmented, coxae widely separated, legs often very long. Wingless, or with elytra of one consistency. Pubescence velvet-like ventrally. The members of this family, often called Pondskaters or Water-striders, live on the surface of water and feed

on aquatic animals and floating débris. As a rule the legs are long, but *Mesovelia*, British, resembles the land bugs. *Hydrometra*, also British, walks on the surface-film holding its body above the water. It is easily drowned. *Velia*, British, prefers rapidly running water. The wingless *Halobates* with some fifteen species is one of the very few genera of insects found in the open ocean. *Rhagovelia* is also marine but found nearer the shore in the Gulf of Mexico. The eggs are usually laid on water plants.

Fam. 10. **Henicocephalidae**. The head is enlarged behind the eyes. Rostrum very short. Elytra entirely membranous and well veined. Front legs swollen. Only one genus *Henicocephalus*, widely distributed with a dozen species.

Fam. 11. **Phymatidae**. Anterior legs short and thick and often devoid of tarsi. Strong predatory bugs. *Phymata* frequents daisies and other flowers with which its colour harmonizes, and it preys upon visiting insects. In some forms the tibia makes with the femur a very efficient form of nipper or grasping claw.

Fam. 12. **Reduviidae**. Short rostrum, in repose lying free from head and looped. Eyes large, ocelli behind eyes. Elytra when present in three portions. Head very movable. Tarsi 3-segmented. A large and important family of over 2,000 species, largely tropical. They are predaceous, living on other insects, and are very varied in shape and colour. *Reduvius*, British, preys on bed-bugs and cockroaches. *Nabis*, British, mimics an ant in its younger stages. *Conorhinus*, *Melanolestes* and *Rasahus* are known to bite man in America, sometimes with serious effects. The eggs of the Reduviidae are usually very characteristic and operculated. The family is said to be free from stink-glands.

Fam. 13. **Aëpophilidae**. Small, with short head and no ocelli. Very short elytra, but no hind-wings, present. This family consists of but one species found in the sea on the coast of France and England.

Fam. 14. **Ceratocombidae**. Minute. Head prolonged in front, ocelli present, eyes close to thorax. Rostrum free. Small and fragile bugs. *Dipsocoris* is found on the stony margins of Scotch streams.

Fam. 15. **Cimicidae**. Flat with very short elytra which often leave



FIG. 436.—*Nabis lativentris*, young. Cambridge. *A* insect seen from above; *B* profile. From Sharp.

the abdomen exposed. No ocelli. Rostrum lies in a groove. A small but widely distributed family with some 12 species, but notorious as it includes the bed-bug *Cimex lectularius*, a long-lived and prolific insect confined to the dwellings of man. Other species infest birds and bats, e.g. *Oreiciacus hirundinis* common in swallows' nests.

Fam. 16. **Anthocoridae**. Small. Head projecting, in front, well in advance of the origin of the antennae. Eyes near thorax, ocelli and elytra usually present. Rostrum free. Plant- and tree-haunting bugs, said to feed on other insects. Fairly numerous both in species and individuals. *Triphleps* eats plant-lice.

Fam. 17. **Polyctenidae**. Elytra short and undivided. Proboscis sheath 3-, tarsi 4-, and antennae 4-, segmented. A small family of three or four species parasitic on bats. *Polyctenes*.

Fam. 18. **Capsidae**. Fair-sized, usually slender. Elytra and wings large. No ocelli. Antennae 4-segmented, the two distal segments slender. Tarsi 3-segmented. Scutellum visible. Ovipositor present. A large family with over 1,000 described species, nearly 200 British. They haunt plants and are at times destructive, though some devour other insects, e.g. *Camptobrochis*. *Oncognathus* is found amongst timothy-grass, *Fulvius* on lichens, *Lygus* causes the "buttoning" of strawberries, *Poecilocapsus* sucks the sap of currants and gooseberries.

Fam. 19. **Saldidae**. Eyes large, ocelli between them. Rostrum free.



FIG. 437.—*Nepa cinerea*.

Scutellum large. Elytra of three parts, covering abdomen. Tarsi 3-segmented. Three genera with about 100 species compose this family. The Saldidae are small, oval, convex bugs which frequent damp places, wet moss, the sea shore and salt-marshes. They run, and some jump, actively, as is expressed in the name of one genus *Velo-cipeda*. *Salda* the chief genus is British.

Series B. **Cryptocerata**. Aquatic bugs with the antennae hidden on the under side of the head or concealed in a groove.

Fam. 20. **Galgulidae**.* Short stumpy bugs with very broad heads. Eyes large. Ocelli present. Hind-legs long, running. A small family of some 20 species which love the damp margins of streams and ponds. No British species. *Pelagonus*. *Galgulus*.

Fam. 21. **Nepidae**. Anterior legs arise from front edge of prosternum and are raptorial. Abdomen ends in a long cylindrical respiratory tube composed of two semi-cylindrical halves. Tarsi 1-segmented. The water-scorpions are large insects falling into two genera, *Ranatra*, slender and twig-like (Fig. 438) and *Nepa*, flattened and leaf-like (Figs. 437, 375). Both have British representatives. The eggs, laid on water-plants, bear peculiar filaments.

Fam. 22. **Naucoridae**. No raptorial legs, or ocelli or respiratory tube. Anterior legs with broad femora inserted at or near the front of the prosternum. Antennae 4-segmented. Oval, swimming bugs with some nine genera and thirty species. *Naucoris* and *Aphelocheirus* are British. *Pelocoris* feeds on land-insects which fall into the water.

* Sometimes termed *Pelagonidae*.

Fam. 23. **Belostomidae.** No ocelli or respiratory tube. Anterior legs inserted near anterior edge of prosternum. Hind-legs flattened with swimming hairs. This family includes the largest bugs and some of the longest of insects. *Belostoma* measures four and a half inches. They are purely aquatic. The front legs are adapted for holding their prey, and they are said to be very destructive to young fish and frogs. *Diplonychus* and *Zaitia* carry their eggs on the backs of the apparently unwilling male.

Fam. 24. **Notonectidae.** Prosternum short so that the anterior legs emerge from near each margin. Pronotum overlaps head. Antennae 4-segmented. Scutellum large. The members of this family, sometimes called "water-boatmen" or "back-swimmers," swim on their back, which is very convex. They prey on insects and fish. They hibernate in mud and lay their eggs on water plants. *Notonecta* and *Plea* have British species.

Fam. 25. **Corixidae.** Head broad, free from pronotum, and very movable. Prosternum short. Common water-bugs, flattened ventrally and swimming the right way up. *Corixa* and *Sigara* are British. The former is so abundant in Mexico, that it is made with meal into cakes and forms a popular article of diet, and is exported to Europe as food for game-birds, etc.

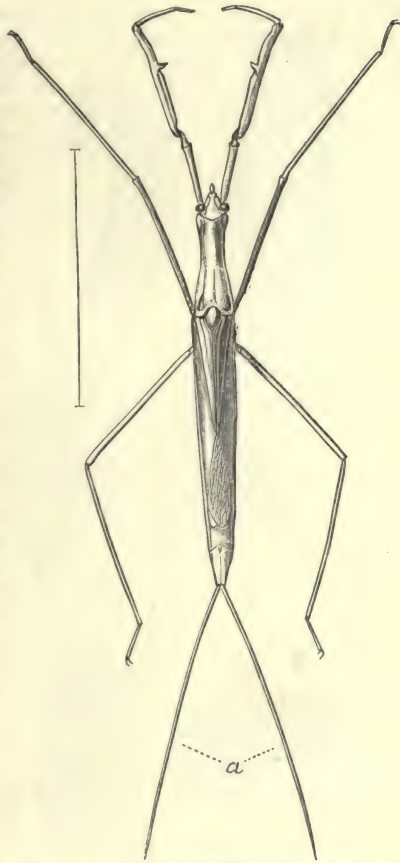


FIG. 433. *Ranatra linearis*, with the two portions, *a*, of the respiratory siphon separated. Cambridge. From Sharp.

Sub-order 2. HOMOPTERA.

The wings all lie upon the body in a roof-like manner and the front-wings are usually of one consistency. The front of the head is bent over so as to touch the coxae.

Fam. 1. **Cicadidae.** Three ocelli, between the eyes. Antennae with short basal segment bearing a 5-segmented filament. Anterior femora thickened and toothed. A group of large and mostly tropical insects (Fig. 439). The wings are usually transparent with many nervures, but are sometimes pigmented. Cicadas are often long-lived, but almost the whole of the life is passed in the larval stage underground. In the case

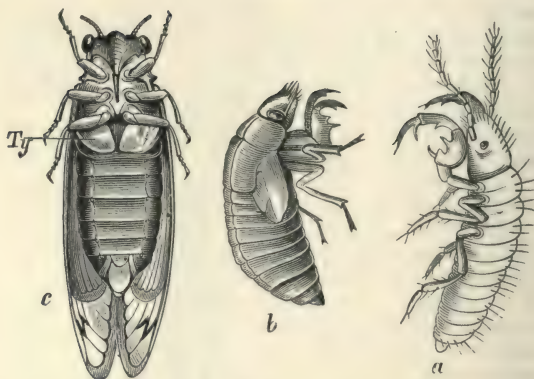


FIG. 439.—*Cicada orni* (after Packard). *a* larva; *b* pupa; *c* male; *Ty* stridulating apparatus.

of *Cicada septemdecim* the larva lives for from 13-17 years according to the temperature and is regarded by some authorities as a very destructive to roots. Its anterior legs are modified for digging through the earth, the antennae are well developed, the skin thin and white

(Fig. 440). The pupa is shorter and more compact. It crawls out of the ground, clasps a plant with its powerful fore legs, splits along its back and the imago steps out. The female lays her eggs by means of an ovipositor in little slits in twigs which are sometimes broken by their additional

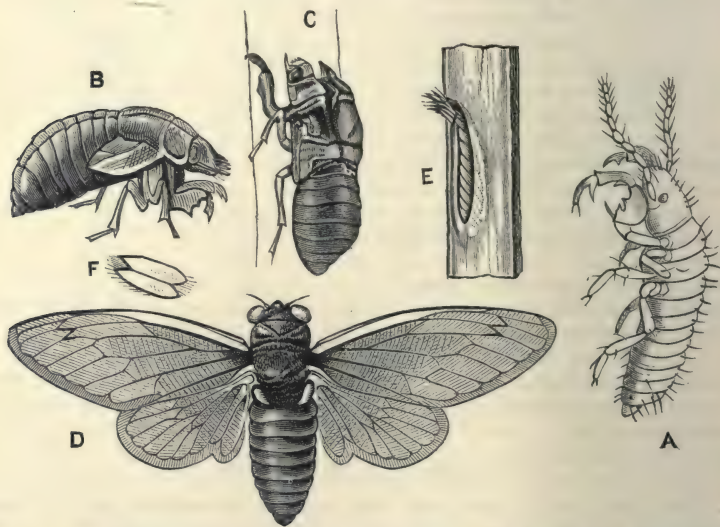


FIG. 440.—*Cicada septemdecim*. North America (after Riley). *A* larva; *B* nymph; *C* nymph skin after emergence of the imago *D*; *E* section of twig with series of eggs; *F* two eggs magnified.

weight. The characteristic and at times overpowering song is produced by a special apparatus on the metathoracic and anterior abdominal segments. *Tympanoterpes* is said to rival a steam engine.

Fam. 2. **Fulgoridae.** Antennae 3-segmented, the terminal one a

hair, inserted beneath eyes. Ocelli usually two. Head sometimes produced into an enormous swelling. Thorax not enlarged. A large and varied family including the so-called Lantern-flies with their curiously enlarged heads. Many excrete a flocculent wax e.g. *Cixius* British and *Phenax*. *Ityraea ormenis* and *Pochazia* resemble Lepidoptera. *Chlorochroa* attacks beetroots. *Scolops*, *Heliocoptera*, *Otiocerus*.

Fam. 3. **Membracidae**. Bizarre looking insects with the prothorax enlarged and projecting backwards. Antennae inserted in front of eyes. Two ocelli between eyes. A numerous and largely tropical family whose curious pronotal processes cause them in many cases to resemble parts of



FIG. 441.—*Fulgora candelaria*. × 1. China. From Sharp.

plants. *Enchenopa* bears a thorn-like projection. *Telemona* frequents Virginia Creepers, *Entilia* the leaves of Sun-flowers, *Ceresa* injures orchards by its mode of oviposition.

Fam. 4. **Cercopidae**. Antennae inserted between eyes. Two ocelli. No pronotal projections. Scutellum rhomboidal. This family includes the Cuckoo- or Frog-spits, the late larval stages producing from their rectum a foamy fluid in which they lie concealed. The adults are termed Frog-hoppers and they jump actively. *Philaenus* is the commonest British genus. *Ptyelus* a Madagascar genus produces so much fluid that five or six dozen larvae will excrete a quart in an hour and a half.

Fam. 5. **Jassidae**. Ocelli two on the front margin of the head. Posterior tibiae spiny. Scutellum triangular. Small or minute insects, usually slender. They frequent low-growing herbage, and are said to injure pasture, e.g. *Deltocephalus*. *Erythroneura* frequents vines, *Agalia* lives amongst garden produce. The eggs are often laid in grasses.

The preceding families of Homoptera have 3-segmented tarsi, the succeeding ones have them 2-segmented, except the *Coccidae* which have but one tarsal segment.

Fam. 6. **Psyllidae**. Minute insects with transparent wings. Antennae long, 8- to 10-segmented. Three ocelli. A large family of small forms about the size of plant-lice but in shape more like Cicadas. They frequent plants and jump actively (Fig. 442). They pass through larval and nymph stages which are marked by change of colour and form. In the nymph the large wing-pads stand out horizontally from the sides of the

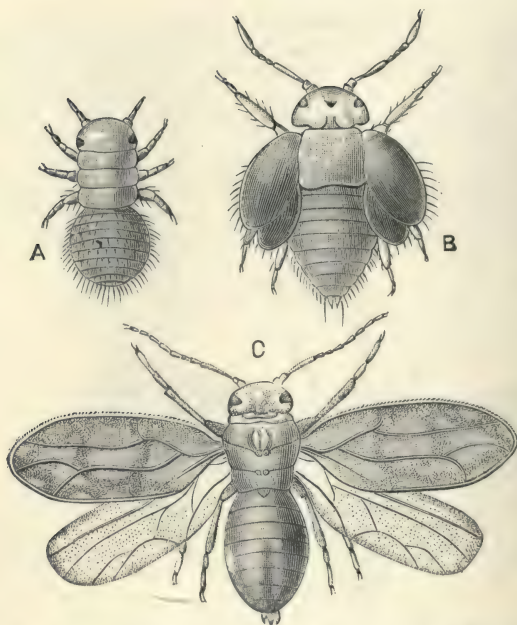


FIG. 442.—*Psylla succinta*. $\times 15$. Europe (after Heeger. From Sharp). A larva before first moult; B larva after third moult; C adult.

certain glands (Fig. 443). The young differ but little from the parents. All through the summer the females reproduce parthenogenetically and viviparously, and as their young are all females and are capable of

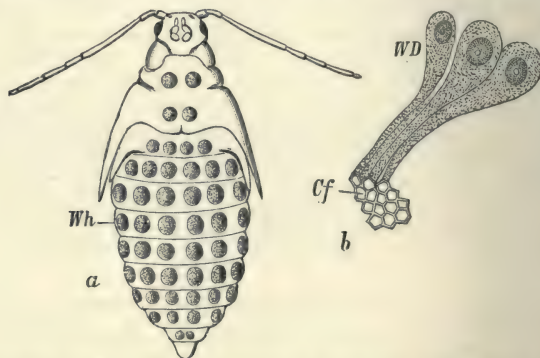


FIG. 443.—The wax glands and the prominences on which they open of one of the *Aphidae* (*Schizoneura Lonicerae*). a pupa seen from dorsal surface; Wh prominences on which the wax glands open; b the unicellular wax glands WD beneath the cuticular facets Cf of the skin.

body. *Psylla* secretes "honey-dew" in such quantities that it has given rise to the legends of weeping trees. Some species form galls, e.g. *Pachy-psylla*.

Fam. 7. **Aphidae**. Minute insects. No ocelli. When present the four pair of wings are transparent. Antennae 3- to 7-segmented. Frequently a pair of processes is borne on the dorsal surface of the 5th abdominal segment. Plant-lice abound both in species and individuals. They are soft bodied and often coated with a waxy "bloom" secreted by

producing offspring in a few days, plant-lice multiply exceedingly. Sooner or later and generally towards the autumn, the plant-lice pro-

duce males as well as females, and then pair. The female gives rise to a fertilized egg which survives the winter and in the spring a parthenogenetic female emerges from this. The relation of the winged to the wingless forms is obscure. As a rule many wingless generations succeed one another and then a generation of winged females suddenly appears and undoubtedly aids in the dispersal of the species. The curious abdominal processes are said to open into the body cavity. They excrete a waxy fluid. The honeydew (so prized by ants, who in some cases have domesticated certain species of Aphides) comes from the alimentary canal. Some genera e.g. *Pemphigus*, *Chermes* (p. 640), *Schizonura* produce galls. *Phorodon* includes the Hop plant louse, *Nectarophora* the green-pea plant louse, *Drepanosiphum* the maple plant louse. *Aphis* is perhaps the best known genus.

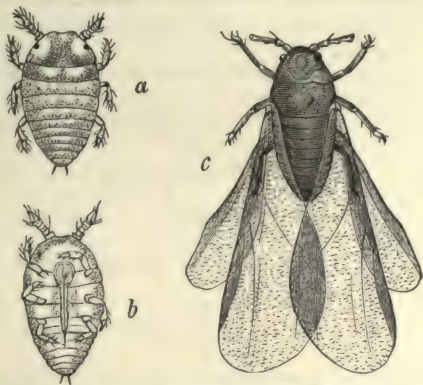


FIG. 444.—*Phylloxera vastatrix*. *a* wingless root louse seen from the back; *b* from the ventral surface; *c* winged form.

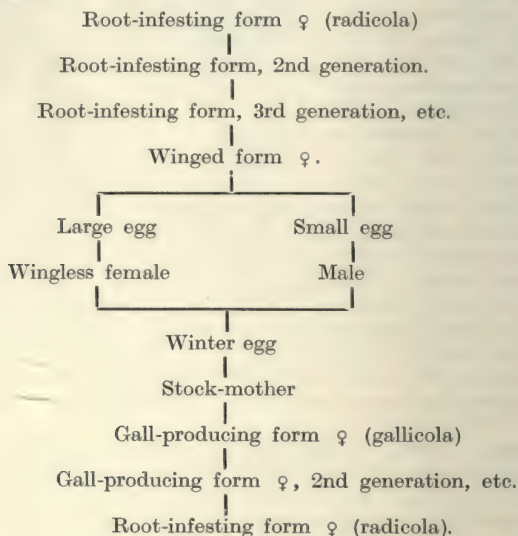
*Phylloxera vastatrix** is the well known enemy to vines and affords a good example of the complicated life-history presented by the Aphidae. The wingless root-dwelling forms—*radicolae*—are found with their proboscis firmly fixed in the tissues of the young roots. They do not move about, but lay little clumps of thirty to forty parthenogenetic eggs, which give rise in six to twelve days, according to the temperature, to young larvae. These moult once or twice, creep about a little, and then fix themselves by their probosces and lay parthenogenetic eggs like their mother. In this way many agamic generations succeed one another, and the rate of increase is so great that it has been calculated that the descendants of a single insect which laid its eggs in March would number twenty-five millions by October.

As autumn comes on some of the eggs give rise to larvae which are provided with the rudiments of wings; before their last change of skin they creep above ground, and then at the final moult a winged female emerges and flies away. This form serves to spread the vine disease from one district to another. It is also parthenogenetic, but lays two kinds of eggs. From the larger of these a female hatches out, whilst the smaller produces in eight or ten days a male. This is the first and only appearance of this sex in the life-history of the *Phylloxera*. The male is devoid of mouth and alimentary canal; it fertilizes the female, which soon after lays a single fertilized egg, the so-called "winter egg." This is deposited in some crevice or crack in the bark of the vine. In the spring a "stock-mother" hatches out of this egg and makes her way to the young buds of the vine, and inserts her proboscis into the upper surface of a

* H. Stauffacher, *Zeitschr. wiss. Zool.*, lxxviii, 1907, p. 131.

leaf. The irritation thus set up causes the formation of a hollow gall on the under surface of the leaf, which opens to the exterior on the upper surface. The stock-mother lays eggs, and her offspring—*gallicolae*—give rise to new galls, but ultimately some of them descend to the ground, burrow beneath it and attach themselves to the roots, and thus become *radicolae*.

The complicated life-history of this form may be expressed by the following table :—



Fam. 8. **Aleurodidae**. Minute. Four white, mealy wings. Antennae 7-segmented, the second segment long. These small insects are usually found on the under surface of leaves. The two sexes are about equally developed and both are winged. There are two genera *Aleurodes* and *Aleurodiscus* with some 150 species. *Aleurodes brassicae* is common on cabbages in Britain.

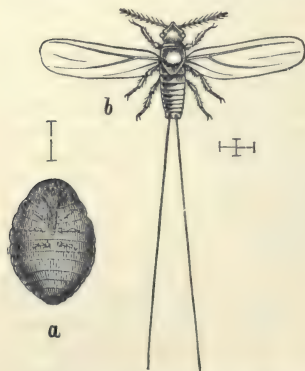


FIG. 445.—*Coccus cacti*. a female; b male (after Burmeister).

Fam. 9. **Coccidae**. The eggs give rise to larvae, which in those cases that have been investigated, are alike; but later development is quite different in the two sexes. The male passes through pupal stages, and finally emerges as a minute insect with only one pair of wings, anal cerci, and with the mouth atrophied. The female becomes very much larger than the male, and never acquires wings; the antennae and legs usually degenerate, the latter sometimes disappearing entirely. Mouth-parts are present in the adult females, which are very fre-

quently stationary on their food-plants, and covered by scales of various forms, composed of cast skins, secretions, etc.

As a rule Scale-insects are seen in the form of these scales attached to fruit, leaves or bark. Under the scale the female lives and lays her eggs. Some species form no scale and are then usually coated with a waxy efflorescence, and are termed "mealy-bugs." The females are very prolific and parthenogenesis exists but not to the extent formerly thought when the males were less well known. Many of the products of scale-insects have a commercial value. *Ceroplastes ceriferus* in India and *Ericerus pela* in China produce white wax, *Carteria lacca* forms lac. *Kermes* and *Porphyrophora* afford a red dye, and *Coccus cacti* (Fig. 445) is the well-known cochineal insect. On the other hand many are injurious to plants: some render the leaves sticky by copious secretions of honey-dew. *Mytilaspis* forms the "oyster-shell" scale on orchard trees. *Aspidiotus* attacks oranges, and there are many others which infest fruit-trees, etc.

Group IV. ENDOPTERYGOTA:

The wings arise by invaginations of the hypodermis, and for sometime remain tucked in the body. Complete metamorphosis.

Order 15. NEUROPTERA.*

Carnivorous insects with biting mouth parts; four membranous wings with many cross-nervures; antennae large. Complete metamorphosis with as a rule an eruciform larva.

The Order Neuroptera has been much diminished in recent years by the recognition of the ordinal value of many of the families which at one time were included in it. Some species have aquatic larvae, but the majority are terrestrial. On the whole the Order is a beneficent one as far as man is concerned inasmuch as its members eschew plants and many of them devour injurious insects. The Order is divided into nine families†:—

Fam. 1. **Sialidae.** A squarish head bearing long antennae. Four wings which when at rest are unfolded and meet at an angle. Fairly numerous nervures break up the wings into many irregular cells. The larva has powerful mandibles and the pupa is quiescent. The Alder-flies comprise but five genera. They haunt the trees and shrubs along the banks of streams. *Sialis lutaria* is a favourite fly with fishermen and is one of the commonest insects in Britain. The eggs are laid in masses of two or three thousand on rushes, grass-stems, etc. The larvae have a pair of

* Dufour, *Ann. Sci. Nat.* (3), ix, *Zool.*, 1848, p. 91. Loew, *Linnaea Entomologica*, iii, 1848. Hagen, *Stettin Ent. Zeit.*, xxvii, 1866, and *P. Boston Soc.*, xv, 1873, p. 263.

† The Neuroptera as here restricted are equivalent to the Planipennia minus the Panorpidæ (Mecaptera).

jointed branchial filaments on each segment of the abdomen, which ends in a median unsegmented style. The pupa is quiescent and the imago lives but for a few days. *Corydalis* and *Chauliodes* are giant forms and the former often has the mandibles of the male enormously enlarged.

With exception of a few South American forms the family is confined to the Northern Hemisphere.

Fam. 2. Raphidiidae.

The posterior part of the head and the pro-thorax are elongated and narrowed, producing the appearance of a long neck. The female has a long ovipositor. The Snake-flies are confined to Europe, Asia and North America. The larvae are carnivorous and prey upon insects frequenting the old and rotten wood in which they live. The pupa, which in appearance is mid-way between a larva

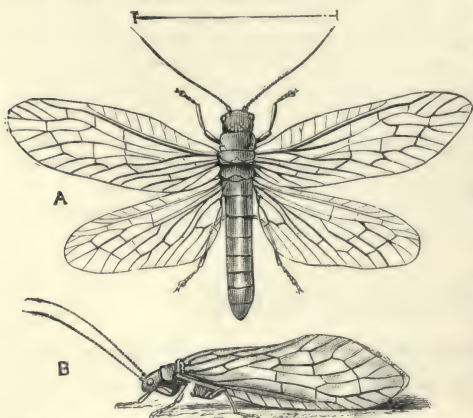


FIG. 446.—The Alder-fly, *Sialis lutaria*. Britain. A with wings expanded; B in profile. From Sharp.

and an imago, becomes active before it gives exit to the latter. There are but two genera, *Raphidia* and *Inocellia* with a fair number of species.

In the remaining families, the mandibles and maxillae are characteristically coadapted in the larva to form piercing and sucking organs.



FIG. 447.—a *Myrmeleon formicarius*; b its larva.

Fam. 3. Myrmeleonidae. Antennae short and clubbed. The nervures of the apex of the wing enclose regular oblong cells. Maxillary palp 5-segmented, labial palp 3-segmented. Nocturnal insects, whose larvae are the well known ant-lions. The eggs are laid in sand, and when the larvae emerge they prepare conical pits in sandy soil and, concealing themselves at the bottom, seize and devour any unwary insect which falls into their pit. The arrangement of their legs necessitates a retrograde motion, and enables them also to throw sand upon their victims to aid their descent into the pit. The prey is grasped in the stout mandibles; these have grooves in which the maxillae play to and fro.

The oral orifice is closed, but the grooves communicate with the alimentary canal, into which they convey the juices of the victims. The stages between larva and imago are passed in cocoons made of sand and silk. There are no British representatives, but several species of *Myrmeleon* (Fig. 447) live on the Continent. Other forms, e.g. *Dendroleon*, hunt their prey on foot. *Palpares* and *Tomateres* are large forms.

Fam. 4. **Ascalaphidae.**

Antennae long and clubbed. The apical cells of the wing are irregular. These insects hawk through the air like Dragon-flies, which they somewhat resemble, especially in the broad base to their posterior wings, but the antennae serve to distinguish them at once. The eggs are laid on blades of grass, to which the imagos cling in dull weather. The carnivorous larvae have enormous mandibles and hunt their prey under stones and leaves. A cocoon is formed. Some thirty genera are recognized which mostly live in warm climates. *Ascalaphus* is found as far north as Paris. *Helicomitus* in Ceylon, *Uhula* on St. Vincent Island.

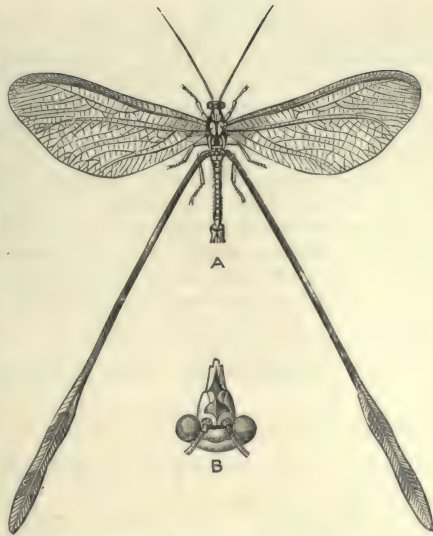


FIG. 448.—*Nemoptera ledereri*. Asia Minor (after Selys). A the imago; B its head seen from in front and magnified. From Sharp.

The eggs are laid on blades of grass, to which the imagos cling in dull weather. The carnivorous larvae have enormous mandibles and hunt their prey under stones and leaves. A cocoon is formed. Some thirty genera are recognized which mostly live in warm climates. *Ascalaphus* is found as far north as Paris. *Helicomitus* in Ceylon, *Uhula* on St. Vincent Island.

Fam. 5. **Nemopteridae.**

Head produced into a beak. Antennae long, but not clubbed. Hind wings much longer and narrower than fore-wings, twice as long as body. A small group of some thirty species of delicate Insects not occurring north of the Mediterranean basin. The larva has an extraordinarily long neck: that of one species, probably a *Nemoptera* (Fig. 448), lives in the sand in the tombs and pyramids of Egypt.



FIG. 449.—a larva of *Mantispa styriaca* after hatching. b the same before the pupal stage (after F. Brauer). c *Mantispa pagana*.

Fam. 6. **Mantispidæ.** Prothorax very long and bearing a pair of raptorial legs at its anterior extremity. The four wings are sub-equal in size with numerous nervures. They serve at once to distinguish this family from the Mantidae, with which they have a superficial resemblance chiefly owing to their raptorial front legs. The antennae are short, not clubbed. The eggs are numerous and stalked; in *Mantispa styriaca* they are laid on stalks or stems. The larvae appear in the autumn and hibernate till the spring, when they make their way into the egg-bags of certain spiders (*Lycosa*); here they feed on the eggs and young spiders, then cast their skins and turn into inert larvae, which spin cocoons inside the spider's egg-cases. After a period of quiescence a nymph makes its way to the outer world and soon gives origin to the imago (Fig. 449). A South American species *Symphrasia varia* makes its home in the nests of a species of wasp. A few species are found in South Europe but the majority prefer a warmer climate.

Fam. 7. **Hemerobiidæ.** Wings at rest folded in a roof-like way over

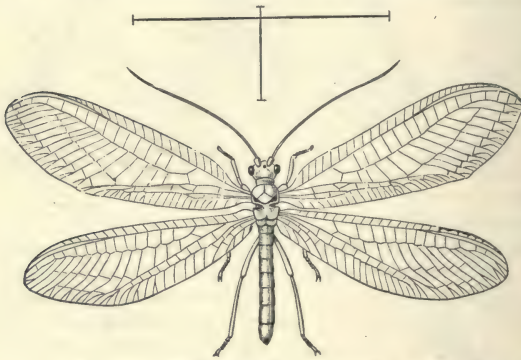


FIG. 450.—*Chrysopa flava*. Cambridge. From Sharp.

the body. Antennae long, moniliform or pectinated, not clubbed. This family is divided into several small groups about the value and life-history of which there is much uncertainty. *Osmylus chrysops*, British, has a semi-aquatic larva which hides under stones or stems at the water edge: it sucks the

juices of other insects and spins a cocoon encrusted with sand, the silk coming from the posterior end of the intestine which in the larva is cut off from the chylic ventricle. *Psectra* has in the male no posterior wings. The larva of *Sisyra* lives in the fresh water sponge *Ephydatia fluviatilis*. The larvae of *Hemerobius* devour plant-lice, and those of some species cover their bodies with the emptied skins of their victims. *Drepanopteryx*, with one British species, is remarkably moth-like and has an apparatus for holding together its hind- and fore-wings as in some moths.

Fam. 8. **Chrysopidæ.** Long, setiform antennae, not moniliform. This family includes what some writers call the "lace-wing flies," whilst others call them "golden-eye flies," applying the term "lace-wing" to the Hemerobiidæ. They are delicate, elongate insects with a metallic sheen on the living eye. Lacewings are common and there are some fifteen British species. They lay peculiar stalked eggs on stems. The larvae eat plant-lice and other insects. Those of some species clothe themselves in the skins of their victims, which are fastened on by minute hooked hairs. Green algae and lichen are attached to the body by the same means. *Chrysopa* is a common British genus (Fig. 450). The imago has a very unpleasant smell and the group is sometimes called "stink-flies."

Fam. 9. **Coniopterygidæ.** Minute. Few cross-nervures on the wings,

which with the rest of the body are covered by a powdery down. These are the smallest of the Neuroptera. The hind wings are unusually small, and the antennae often unusually long, many times longer than the body. The larva of a species of *Aleuropteryx* lives on Pine-trees and sucks out the contents of the Coccid, *Aspidiotus abietis*, which infests these conifers. Like the Hemerobiidae they form silken cocoons. *Aleuronina* lives on maples. *Coniopteryx* is British.

Order 16. MECAPTERA (PANORPIDAE).*

Head bearing a distinct beak, this is bent down and carries, near the free end, the palpi; antennae long and slender; wings long with many radiating and few cross nervures. Larvae with true legs and pro-legs. Carnivorous.

This Order contains but one family, the Panorpidae, with the characters of the Order. The beak is largely derived from the clypeus and the mandibles are borne at its extremity. The abdomen is long with nine distinct segments. In *Panorpa* it can be reflected over the back in the male, and gives the Order the name of Scor-



FIG. 451.—*Panorpa communis*.
Nat. size.



FIG. 452.—*Panorpa communis*, male. Cambridge.
From Sharp.

pion-flies. There are some ten genera: *Panorpa*, *Boreus* and *Bittacus* are European and North American, and the first two are British. The eggs seem to be laid in moist earth, and the larvae which appear in about a week resemble the young of Saw-flies. They have biting mandibles and maxillae with palps, three pairs of thoracic legs and a pair of pro-legs on the first eight abdominal segments. The larvae are active for a month, then

* Dufour, *Mem. Ac. Sci. étrang.*, vii, 1841. M'Lachlan, *Ent. Mon. Mag.*, 1894.

torpid. After some weeks they change into motionless pupae with free limbs. *Boreus* is devoid of pro-legs in the larval stage, and of wings in the adult. *Bittacus* resembles a Daddy-long-legs and has very long limbs.

Fam. 1. **Panorpidae.** With the characters of the Order. *Panorpa*, *Bittacus*, *Boreus*.

Order 17. TRICHOPTERA.*

Body and wings covered with fine hairs; the latter with few nervures arising from one another at very acute angles; hind-wings larger than fore-wings with a well marked anal area; antennae thread-like; mandibles absent. Larvae caterpillar-like; they usually construct a case to live in. Pupa like an immature imago and active just before the last ecdysis.

The Caddis-flies have their two pairs of maxillae united to form a sucking tube. The meso-thorax is bulky: the large coxae of the anterior legs arise close together. There are nine distinct abdominal segments and the last bears a pair of pincers



FIG. 453.—*Phryganea striata*.

in the male. The moth-like imagos are weak on the wing and haunt the shady margins of the streams from which they emerge. Mandibles, though absent or obsolete in the imago, are present in the pupae as well as the larvae. The eggs are laid, in jelly-like clumps of a hundred or so, in the

water. The newly hatched larvae at once set about building the well known caddis-worm cases, from which they protrude only the head and thorax, a strong pair of hooks at the end of the body serving to anchor the larva in its case. The larvae breathe by abdominal tracheal gills; they live many months and in some cases through the winter; they are largely vegetarians but at times eat other insects. During the period of pupation the

* McLachlan, *Tr. Ent. Soc. London* (3), v, 1865, and *Monographic Revision of the European Trichoptera*, 1874-80. Lucas, *Arch. Naturg.* lix, p. 285, 1893.

case is closed at both ends. For a time the pupa is quiescent; then a nymph emerges and makes its way through the water to some stem. This it ascends, splits its skin and gives exit to the imago, which flies away and pairs. *Enoicycla* has in the female only rudiments of wings; and the hind pair are absent in *Thamastes*. The Trichoptera show affinities with the Lepidoptera, and it is not improbable that the latter have been derived from them.

This order contains some 500 species, about 150 British forms and as many North American—divided into seven families:—

Fam. 1. **Phryganeidae.** The largest forms. Maxillary palps of male hairy and 4-segmented. Antennae and legs stout. The members of this family inhabit still water. The branchiae of the larvae are filamentous. The larval cases are composed of bits of plants and leaves. They live in temperate regions. *Phryganea*, *Neuronia*.

Fam. 2. **Limnophilidae.** Fairly large forms. Ocelli present. Maxillary palps of male 3-segmented. There is a great variety in the form of the cases; *Enoicycla* passes its larval life amongst damp moss. *Apatania* is said to be parthenogenetic.

Fam. 3. **Sericostomatidae.** Maxillary palps of male 2- or 3-segmented. No ocelli. Larvae chiefly live in streams and form their cases of sand and stones. The genus *Helicopsyche* forms a spiral case something like a small snail's shell. *Sericostoma*.

The following four families have 5-segmented maxillary palps in both sexes:—

Fam. 4. **Leptoceridae.** Long antennae. Very hairy palps with the last segment flexible and simple. Larvae make straight or curved cases of sand. The branchiae are short tufts. They resemble the Tineid moth *Adela*. *Odontocerum* is British.

Fam. 5. **Hydropsychidae.** Rather hairy palps with the last segment long and jointed. The larvae inhabit streams and make fixed cases, at the entrance to which some species, e.g. *Rhyacophylax* and *Hydropsyche* spin silken nets to entrap the insects on which they feed. The larvae of British species of *Philopotamus* and of *Tinodes* are said to be without branchiae.

Fam. 6. **Rhyacophilidae.** Palps with very few hairs, the last segment simple and cylindrical. Some larvae of this family have no branchiae and breathe by stigmata. They live in rapid streams and make fixed cases under stones. *Rhyacophila*.

Fam. 7. **Hydroptilidae.** Small forms very like Tineid moths. Wings narrow. The larvae make small seed-like cases, and they have no branchiae. *Oxyethira* fastens its case to leaves of water-lilies. *Hydroptila*.

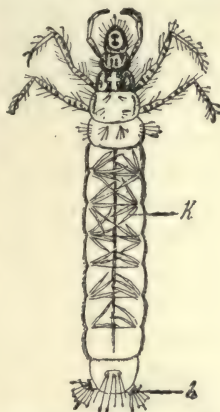


FIG. 454.—Larva of *Phryganea fusca* (after Pictet).
h grasping hooks; k tracheal gills.

Order 18. LEPIDOPTERA.*

The wings and body are covered with a multitude of flattened scales which cause the brilliant colours and patterns on the four wings; nervures rather few, not more than fifteen reaching the edge of the wing, only four cross-nervures exist; mandibles as a rule absent or vestigial, the first maxillae elongated and grooved so as to form a long coiled, tubular proboscis. Metamorphosis complete; the larva, a caterpillar, has large mandibles. The appendages of the pupa are pressed against and are usually adherent to the body.

The Lepidoptera include the Moths and Butterflies, the most

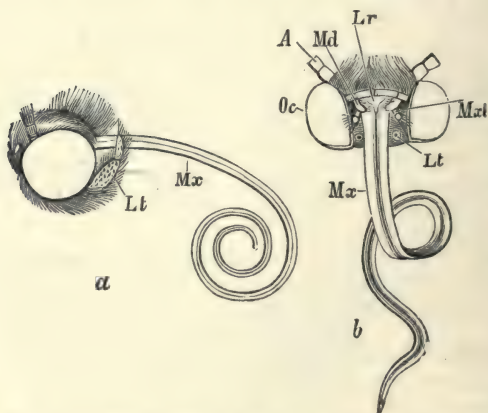


FIG. 455.—Mouth-parts of butterflies (after Savigny); *a* of *Zygaena*; *b* of *Noctua*; *A* antennae; *Oc* eyes; *Mxt* maxillary palp; *Mx* maxilla; *Lt* labial palp; *Lr* labrum; *Md* mandible.

beautiful of all insects. The head of the imago is large and a good deal of its surface is taken up by the great compound eyes, which may be supplemented by a pair of ocelli. The antennae are large and have many segments. The labrum is large, the mandibles in most cases indistinguishable.

The maxillary palp is also much reduced, but the maxilla—though exactly what part of it seems uncertain—is prolonged into a semi-cylindrical process which with its fellow forms the coiled and protrusible proboscis which may be several inches in length. In some forms however the maxillae are absent or they may remain as delicate processes hanging from the mouth and independent of one another. The labium is much reduced but its palps are enlarged and form conspicuous tusk-like, hairy structures. The mouth seems to be

* Scudder, *Butterflies of New England*, 1889. Staudinger, Schatz and Röber, *Exotische Tagfalter*, Furth, 1884–7. E. Reuter, *Acta. Soc. Fen.*, xxii, 1896. Bates, *Jour. Ent.*, i, 1862. Müller, *Zool. Jahrb. Syst.*, i, 1886, p. 417. Hampson, *Monograph of the Phalaenae of the World*, Brit. Mus. E. Meyrick *Handbook of British Lepidoptera*, 1895.

closed in certain species and the stomach sometimes aborted, but other species suck up the sap and juices of plants by means of a pumping organ in the head.

The three thoracic segments are firmly fused together. The prothorax is reduced to a mere ring, but bears on its upper side a pair of process termed patagia. The mesothorax is very large and is bounded behind by a large scutellum. Just in front of the insertion of the fore-wings the mesothorax bears on each side a small flap, the tegula, which overhangs the articulation of the wings. The metathorax is comparatively small. In the female seven abdominal segments may be made out; two more, and possibly a trace of a tenth, are tucked into the seventh. In the male eight segments are externally visible. The legs are slender, covered with scales; the tarsi have five segments.

The fore-wings are larger than the hind-wings; in some species both pairs appear larger than they are owing to the scales overlapping the edge of the wings. The males are invariably winged, but in rare cases, e.g. the Winter moth *Cheimatobia brumata*, the female is wingless. The fore- and hind-wings of each side are either correlated by a bristle—the frenulum—projecting from the latter and fitting into a flap or a bunch of stiff hairs—the retinaculum—on the former; or the hind-wing has a shoulder projecting forward under the base of the front wing; or thirdly, in some moths without a frenulum, the fore-wing has a small lobe at its base, called the jugum, which droops towards the hind-wing, and which may slightly help the two to work together. Each wing has almost always one *cell*, or area completely surrounded by nervures; the latter are much more numerous at the outer margins than at the bases of the wings.

There is a pumping apparatus divaricated by muscles in the head; the oesophagus traverses the thorax and opens into a tubular stomach, which is preceded by a crop. A diverticulum erroneously called a sucking stomach opens into the oesophagus. The intestine is slightly coiled and ends in a large rectum. Three malpighian tubules open by a common duct into each side of the alimentary canal. The heart is looped both at its point of entry, and within the thorax. There are three thoracic ganglia close to one another and four abdominal ganglia. As a rule there are four egg-tubes in each of the two ovaries, and the two oviducts open by a single orifice at the end of the body. In front of this on the

eighth abdominal segment is the opening of a bursa copulatrix which communicates internally with the oviduct and which may be enlarged to form a spermatheca. There are also accessory glands. The two testes of the male lie in a common capsule; the vasa deferentia unite to form an ejaculatory duct. The eggs are very varied in colour and sculpture and range from a few dozen to several thousand in number. They may be deposited promiscuously, or they may be carefully laid on the food-plant of the ensuing larva, which makes its exit after a period varying from a few days to a few months.

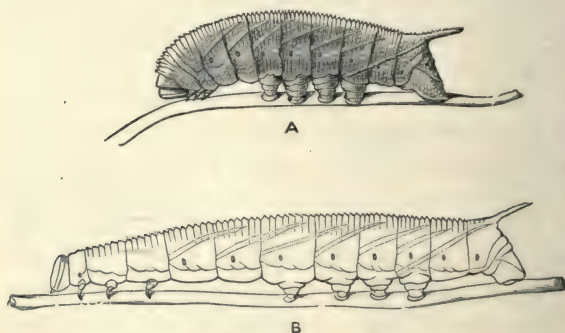


FIG. 456.—Larva of the Poplar Hawk-moth, *Smerinthus populi*.
 $\times 1$. A in repose; B in movement. From Sharp.

The larva is popularly known as a caterpillar. It has a head followed by three segments—the thoracic—bearing true legs, and ten abdominal segments, the

last of which is in some cases difficult to make out. The abdominal segments bear a varying number of tubular feet, each ending in a circle of small hooks, and the body terminates in a somewhat enlarged pair of similar processes. The larva is essentially the feeding stage of the insect, and its stomach is very large. The silk glands are also extensive; they open by a common duct in the middle of the labium on the spinneret, which is by some homologized with the hypopharynx. Contrary to what obtains in the imago, the mandibles are large and the maxillae and labial palps small.

The pupa, often termed a chrysalis, reaches its fullest development in this Order. Its skin hardens and the appendages of the body are glued to the outside. It is incapable of movement except for a slight wriggling of the posterior segments. It may be exposed, and has in that case often patches or knobs of a brilliant metallic lustre, or it may be concealed in a cocoon of silk with which some species incorporate extraneous materials.

In many forms the body of the pupa ends in a projection—the cremaster—and when the pupa is one which hangs suspended from a twig or leaf the cremaster is provided with a number of minute hooks. Various methods are used for the imago to escape from the cocoon. After emergence it rests for a while for the wings to dry and then flies away.

The great beauty of the Lepidoptera is due to the scales, which are little flattened sacs of chitin of very various shape. Some contain pigment, which in certain species take the form of urates. Waste nitrogenous matter is not uncommonly utilized as pigment, as in the case of a family of Polychaets, the Capitellidae, and perhaps some Tunicates. The white glistening scales are said to contain air. The metallic burnish of some butterflies is due to the minute ridging of the surface of the scales, which, acting as diffraction-gratings, splits up the light.

There are perhaps some 50,000 species described of which some 2,000 are British.

The division of the Order into Butterflies (Rhopalocera) and Moths (Heterocera) is probably not a natural one, but there is a certain convenience in adopting it. Beyond this the Order is subdivided into more than fifty families.

Series 1. RHOPALOCERA. Butterflies.

Antennae clubbed; the hind-wing has no frenulum, but a shoulder projecting forwards under the base of the fore-wing.

Fam. 1. **Nymphalidae.** The anterior legs of both sexes so reduced as to be useless for walking; in the male but a single tarsal segment. The pupa hangs freely, without a girdle, from some support, and is comparatively soft-skinned. This is the largest family of butterflies and in it the pupa attains the height of its development. This stage is frequently ornamented with gold or silver bosses. The family is divided into eight sub-families:—

Sub-fam. 1. **Danainae.** The anal (inner margin or submedian) nervure of the front wing forked at its base. Cells of hind-wing closed. Front feet of female end in corrugated knobs. Larvae smooth but with fleshy protuberances.

Large rather black or purplish butterflies which chiefly live in warm climates though they extend far north in America. There are some seven genera; *Limnas*, *Anosia*, *Danais*.

Sub-fam. 2. **Ithomiinae.** Front foot of female has a tarsus, though a shortened one. The larvae have no long processes. This



FIG. 457. *Ithomia pusio*. Brazil.
From Sharp.

sub-family is found only in tropical America. The wings have very few scales in *Hymenitis* and *Ithomia*, though those of *Tithorea* and others have many.

Sub-fam. 3. **Satyrinae**. Compressed palps with long, stout hairs. Cells of wings closed and one or more nervures of front-wings swollen. The larva is smooth or with few hairs, stout in the middle and bifurcated at the posterior end. A large group of usually small, grey and brown butterflies with feeble flight, found all over the world. The pupae are often suspended without a girdle, but sometimes lie loose on the ground or enclosed in a thin cocoon, that of the Grayling *Hipparchia semele* is sometimes found in the ground. *Erebia*, *Coenonympha*, *Melanargia*, *Pararge*, *Satyrus*, *Epinephele* are British genera. *Haetera*, *Cithaerias*, *Pierella*.

Sub-fam. 4. **Morphinae**. No cell on the hind-wing. Larvae smooth or spiny with the posterior end of the body forked. This sub-family is confined to the tropics of Asia and America, and is well known by the brilliant blue butterflies of the genus *Morpho* with some fifty species found in the forests of South America. The caterpillars of some species are gregarious.

Sub-fam. 5. **Brassolinae**. Large forms with the cell in both pairs of wings closed and sometimes a second closed cell in the hind-wing. On the under surface are often large eye-spots. Larvae not very spiny, stout in the middle with a bifurcated tail. A small South American family with the curious habit for a butterfly of resting during the day. *Caligo*.

Sub-fam. 6. **Acraeinae**. Cells closed, anal (inner margin or submedian) nervure unforked. Palps plump and hairy. Larvae with long branching hairs. Moderate sized, not striking butterflies, largely African, but with Oriental and South American species.

Sub-fam. 7. **Heliconiinae**. Bright butterflies with narrow wings. Anal (sub-median or inner margin) nervure not forked. Cell of hind-wing closed. Palps compressed, scaly at sides hairy in front. The male has a long unjointed tarsus, the female a 4-segmented one in the front-legs. Larva with branched spines. Tropical American with two genera *Heliconius* and *Eueides*. The pupae are unusually spiny.

Sub-fam. 8. **Nymphalinae**. Cells imperfectly closed or completely open. Front tarsus of the male with but one segment, not spiny, of the female 4- or 5-segmented. Larvae spiny, or when smooth with bifurcated tail and a horned or spiny head. A large sub-family of 150 genera of world-wide distribution: it is in fact the predominant group. Eighteen species are British. *Ageronia*; *Pyrameis*; *Araschnia*, which produces each summer two generations markedly unlike one another; *Kallima* the dead-leaf butterfly. *Argynnis*, *Melitaea*, *Apatura*, *Vanessa* and *Limenitis* are British.

Fam. 2. **Erycinidae**.* Front-legs of male reduced, tarsi unsegmented and without claws; those of female small but perfect. A family characteristic of tropical America, with one European and British genus *Nemeobius*. Usually small forms, very varied in size and shape. They are divided into two sub-families.

Sub-fam. 1. **Erycininae**. Palps moderate in size. This sub-family includes all the genera but one.

* The Lemoniidae of some authorities

Sub-fam. 2. **Libytheinae**. Palps very long and standing out from head. A single genus *Libythea* with some twenty species is spread throughout the warmer districts of the globe.

Fam. 3. **Lycaenidae**. Front legs but little shorter than the others. Front tarsus in male with one segment bearing but one claw. Claws not toothed. Antennae emerge close to one another. Usually smallish, slender butterflies, the "Blues" of popular nomenclature. Larvae short and hairy. The pupae are also somewhat squat, and besides being supported by the cremaster they are usually made fast by a silken thread which engirdles the middle of the body. It is a large family with eighteen British species. *Lycaena*, *Thecla* and *Polyommatus* are British. *Liptena*, *Vanessa*, *Mimacraea*.

Fam. 4. **Pieridae**. Six legs equally developed. Claws bifid or toothed. A median structure of varying shape called the empodium is present between the claws. A large family of moderate sized butterflies including the Whites and Yellows, Brimstones, and Orange-tips. The caterpillars are cylindrical and downy and usually greenish. The larva fixes itself by its tail with its head upwards and the pupa is lashed to the support by an encircling girdle. The distribution is world-wide. *Euchloe*, *Aporia* and *Pieris*, *Leucophasia*, *Colias* and *Gonepteryx* are British genera.

Fam. 5. **Papilionidae**. Legs fully developed. Front tibia, each with a pad. Claws simple. No empodium. Inner margin of hind-wing concave. Metanotum free. This family includes the most splendid butterflies and is of world-wide distribution. The sexes often differ widely in form and colour. The larvae are cylindrical, not hairy, and have a curious retractile Y-shaped tentacle which can be protruded just behind the head. The pupa is suspended as in the Pieridae. *Papilio* by far the largest genus, *Ornithoptera*, *Thais*, *Leptocircus*, *Parnassius*. There is one British representative, *Papilio machaon*.

Fam. 6. **Hesperiidae**. Legs perfect. Metanotum not free, largely concealed by mesonotum. Front tibia bears a pad. Claws short, toothed at the base. Empodium present. The "Skippers" are butterflies of medium or small size with largish bodies and of a prevailing brown colour. Their head is broad; their antennae arise far from one another, and are thickened before the tip but not really clubbed; their eyes are prominent. Some fly with exceeding rapidity. Many have a brief, jerky flight. The caterpillars have a broad head and narrow thoracic segments, then the body thickens again. They weave webs or fasten together leaves in which they lie hidden, and in these shelters turn to pupae, which are in some species protected by a weak cocoon. The larvae have complete rings of hooks on their abdominal legs and in this and in many other respects they approach the larger moths. This family is a large one with some 200 genera: it is almost world-wide in its distribution. *Syrichthus*, *Nisoniades*, *Hesperia* and *Carterocephalus* are British.

Series 2. **HETEROCERA**. Moths.

Antennae very rarely clubbed; and in the exceptions to this rule, as well as in the great majority of other cases, a frenulum is present.

Fam. 7. **Castniidae**. Antennae knobbed or hooked. Nervures of fore-wings complex and forming accessory cells. Frenulum present. A small family of day-flying moths found mainly in Central America, Australia and the Malayan States, intermediate in many respects between Rhopalocera and Heterocera. The caterpillars live on stems and roots

and are devoid of spines. *Castnia* makes a cocoon of scraps of plants. *Megathymus* is North American.

Fam. 8. **Neocastniidae.** Resemble the preceding family but for the absence of a proboscis. *Tascina* and *Neocastnia*, from the Oriental region, compose the family.

Fam. 9. **Saturniidae.** No frenulum or proboscis, first maxillae aborted. Antennae bipectinate in male. This large and cosmopolitan family resembles the *Bombycidae*, but has only one anal nervure in the hind-wing and only three radial nervures in the fore-wing. Both pairs of wings have transparent areas. Some species, e.g. *Coscinocera* and *Attacus*, are enormous, and the hind-wings are prolonged into extensive tails in *Arceina*, *Copiopteryx* and others. The larvae have ten pro-legs and bear many tubercles with spines. The cocoons vary from a light network to a dense silky covering, which in some cases has a commercial value as Tussore silk. There are some seventy genera, of which but one species *Saturnia pavonia*, the Emperor Moth, is British.

Fam. 10. **Brahmaeidae.** Distinguished from the preceding by the presence of a proboscis. Large dull moths, whose larvae form no cocoons. There is but one genus *Brahmaea* which extends from Japan to Northern Africa.

Fam. 11. **Ceratocampidae.** Large insects, with in the male bipectinate, in the female filamentous, antennae. First maxillae short. The larvae are both hairy and spiny. No cocoon. The imago is mottled with red and yellow markings. Found chiefly in the Southern United States. *Citheronia* is the best known genus.

Fam. 12. **Bombycidae.*** Small, dull moths, as in the Saturniidae, with no proboscis and no frenulum, but with two or three anal nervures on the hind-wing. The first maxillae and the labial palps are reduced. Antennae bipectinate in both sexes. This widely distributed family comprises the true silk-worm moths, which are amongst the few insects domesticated by man. The larvae have ten pro-legs and are not hairy. The true silkworm, whose cocoon yields the silk, is *Bombyx mori*.

Fam. 13. **Eupterotidae.** Large moths agreeing with the *Bombycidae* in the condition of the antennae and of the first maxillae, but with a frenulum. Four radial nervures on the fore-wing and two anal on the hind-wing. The larvae are hairy, and if handled their hairs are apt to break off and prove extremely irritating. They form great webs or nests in which some species, e.g. *Anaphe*, spins its cocoons. The caterpillars of the South American *Palustra* are aquatic, and some species pupate under water. There are no British species, but the Processionary moth, *Cnethocampa processionea* and *C. pinivora*, whose larvae march in a wedge-shaped army led by a single leader, is common on the Continent.

Fam. 14. **Perophoridae.** A small family including the members of the American genera *Perophora*, *Mamillo* and *Lacosoma*, with a score of species. The larvae make little cases of leaves or excrement in which they live apart.

Fam. 15. **Sphingidae.** Stout largish moths with usually a very long proboscis. Frenulum present. Antennae spindle-shaped and often ending in a hook. Front wings usually pointed at tip and long, hind-wings small. The Hawk-moths form a large and cosmopolitan family,

* Most entomologists give a wider interpretation to this family; here it is restricted to the silk-worm moths.

whose larvae are interesting both in their coloration and in the peculiar attitudes they assume. They usually bear a horn posteriorly and dorsally. The pupa comes to rest in the earth and is unprotected by a cocoon. *Acherontia atropos*, the Death's head moth, gives out a curious squeak. Other British genera are *Sphinx*, *Deilephila*, *Choerocampa*, *Smerinthus* and *Macroglossa*.

Fam. 16. **Coccytiidae**. A very small family of one genus *Cocytia* with some four species confined to a limited region of New Guinea. They are very rare and little is known of their life-history.

Fam. 17. **Notodontidae**. Largish moths whose filamentous antennae are sometimes pectinate in the male. The sub-costal nervure of the hind-wing leaves the radial after the middle of the cell. This is a large family, including some species with peculiar larvae. These are in some cases without the last pair of pro-legs, and the hinder end of the body is carried in an elevated position which is enhanced in the Puss-moth caterpillar (*Cerura vinula*) by the protrusion of a pair of extensile tubes. Tubercles or humps are common on the dorsal surface which accounts for the common name "Prominents." Some species, as *C. vinula*, spin tough cocoons, which are softened by an outpouring of a corrosive fluid from the alimentary canal of the emerging imago. Many species have naked pupae which pupate underground. The imagos are as a rule stout with hairy legs and inconspicuous coloration. They are almost cosmopolitan, but are not found in New Zealand and Polynesia. *Gluphisia*, *Ptilophora*, *Pterostoma*, *Lophopteryx* and *Notodonta* are British genera.

Fam. 18. **Cymatophoridae**. The second median nervure of the fore-wing emerges from the cell mid-way between the first and third. The emergence of the other nervures is not evenly spaced. Frenulum and first maxillae well developed. Antennae filiform. This family is small, and its members nocturnal in their habits. In structure it approaches the *Noctuidae*. It is well represented in the Northern Hemisphere. *Thyatira*, *Cymatophora* and *Asphalia* are British.

Fam. 19. **Sesiidae**. Antennae clubbed, first maxillae well developed but with no palps. Frenulum present. Three anal nervures in hind-wing, one and a portion of a second in the fore-wing. The Clearwings are remarkable for large transparent areas, often on both pairs of wings, free from scales. This gives a superficial likeness to some of the Hymenoptera. The larvae have ten pro-legs. They burrow into and eat wood, and being thus concealed are hairless and without colour. The pupa has its limbs comparatively free and is unusually mobile; it is protected by a cocoon of small wood chips. The imagos fly by day. British genera are *Sesia* and *Trochilium*, and doubtfully *Sciapteron*.

Fam. 20. **Tinaegeriidae**. The wings inserted far back on the thorax as in *Sesiidae* but the shape of the wings and wing-fringes resemble those of the *Tineidae*. An exotic family only recently recognized and about which little is known. *Oedematopoda*.

Fam. 21. **Syntomidae**. Fore-wings much longer than hind-wings, in which respect this family resembles the *Zygaenidae*, but transparent spots due to absence of scales are found on the dark-coloured wings. Bipectinate antennae in the male. A family of day-flying moths which frequently resemble Hymenoptera. Like the latter their body is often highly decorated, and in some species drawn out into a long slender structure like an ovipositor. The larvae have tufts of hairs and form a silken cocoon. No British species. *Trichura*, *Naclia*, *Syntomis*, *Dycladia*.

Fam. 22. **Zygaenidae**. The fore-wings (with three anal nervures, two of which are confluent) are longer and not so broad as the hind-wings. The latter have three distinct anal nervures. Frenulum present. Antennae thicker before the tip and then tapering, very flexible. The Burnet-moths are day-fliers with conspicuous metallic coloration. The black and yellow larvae generally have ten pro-legs and feed openly on plants. The pupa is unusually soft and mobile, but is enclosed in a hard cocoon, spun on the food-plants. The family is a large one and widely distributed. *Zygaena* and *Ino* are British.

Fam. 23. **Himantopteridae**.* Scales imperfect and hair-like. Hind-wings form long slender tails which give an un-moth-like look to the insects. This is a small family whose representatives are found only in Africa and India.

Fam. 24. **Heterogynidae**. Intermediate between the *Zygaenidae* and the *Psychidae*. The female imago is very imperfectly developed and remains attached to the pupa-case, in which she is fertilized and deposits her ova. The male is a small moth with imperfect scales. *Heterogynis* of Southern Europe is the only genus.

Fam. 25. **Psychidae**. Females very imperfectly developed, wingless and often legless. Males winged with bipectinate antennae, degenerate mouth-parts and imperfect scales. Smallish moths, widely distributed. The larvae construct cases with a lining of silk and an outer coating of bits of wood, leaves, etc.; these cases may be coiled like Mollusc shells. The female does not quit the case but pupates and lays her eggs there. The degree of development she attains varies in different species. The males fly actively, sometimes in swarms, but do not live long. *Psyche*, *Taleporia*, *Epichnopteryx*, *Fumea*, *Solenobia*, represent the family in the British area.

Fam. 26. **Cossidae**. Mouth much reduced or aborted, no proboscis. The nervures resemble those of the *Zygaenidae*, but the median nervure of the discoidal cell forks. Frenulum present. A small

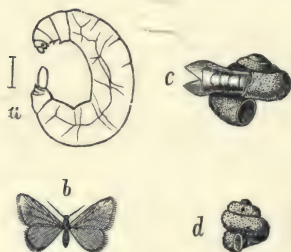


FIG. 458.—a female of *Psyche helix*; b male; c case of the male caterpillar, d of the female.

but widely distributed family of largish moths most abundant in the tropics. The larvae burrow into wood and do great damage to some trees. They are usually hairless and with but little adornment, and are said to live for some two or three years. The pupa is surrounded by a cocoon of chips lined with silk; in some species it is strengthened by a clayey deposit. The goat-moth *Cossus ligniperda* which receives its common name from the smell of the larva, the Wood-leopard moth *Zeuzera aesculi*, and *Macrogaster castaneae*, represent the family in the British area.

Fam. 27. **Arbelidae**. Differ from Cossidae chiefly in absence of frenulum and in greater simplicity of nervures. A small family.

Fam. 28. **Chrysopolomidae**. Nervures as in Cossidae but the imagos resemble *Lasiocampidae*. It includes one genus found in Africa.

Fam. 29. **Hepialidae**. The nervures of fore- and hind-wings closely similar. Scales imperfect. Jugum present. No frenulum. Maxillae at

* Thymaridae of some authorities.

any rate very much reduced, if not absent; antennae extremely short. The mouth parts are altogether rudimentary and no food is taken by the imagos. The Swift-moths form a small but varied family, zoologically very isolated. The members of it vary greatly in size, from small moths to insects six or seven inches in breadth across the wings. The larvae live on roots or the wood of trees and are usually bare, the pupae are also subterranean and capable of moving through the earth. In many anatomical details the Hepialidae show a great simplicity of structure, e.g. the testes remain distinct, the nerve-chain and heart show less concentration than in other moths, the tracheal system resembles that of the larva, the nervuration of the fore- and hind-wings is similar. Some species of the only British genus *Hepialus* differ markedly in the appearance of the two sexes, but this difference is not constant and varies greatly in different localities. The Australian region seems to have most species, but the family is cosmopolitan.

Fam. 30. **Callidulidae.** The wing nervures resemble those of the Pyralidae. Frenulum absent or rudimentary. This is a small family of day-flying, light moths resembling butterflies. It is confined to the south-east half of Asia and the neighbouring islands.

Fam. 31. **Drepanulidae.** Apex of fore-wing pointed or hooked in many cases. Frenulum sometimes wanting. No maxillary palps, and labial palps small. A small but cosmopolitan family. The larva has but eight pro-legs and terminates in an up-turned process somewhat as do the larvae of certain *Notodontidae*. The hooks on the pro-legs do not form a complete circle. The cocoon is weak and formed amongst leaves. *Drepana* and *Cilix* (which has one species that at rest resembles a bird's dropping) represent the family in Britain.

Fam. 32. **Limacodidae.** Allied in nervuration to the *Zygaenidae*, but the sub-costal nervure anastomoses with the radial and is not united to it by a cross-nervure. First maxillae reduced. Small, squat moths of varying appearance which take no food in the imago state. Nocturnal. The larvae have no pro-legs and are flattened and somewhat slug-like. They eat leaves, but except when feeding the head is withdrawn into the body. The elaborate cocoons are often attached to twigs or leaves, and provided with a lid through which the imago emerges. They are mainly a tropical family, but *Heterogenea* and *Apoda* (*Limacodes*) are British.

Fam. 33. **Megalopygidae.** Wing nervures resemble *Zygaenidae* but in the fore-wing the three anal nervures are for the most part distinct. A small family with very hairy larvae and imagos. The former are said to have seven pairs of pro-legs. The cocoon is fitted with a lid. American. *Megalopygè* and *Lagoa*.

Fam. 34. **Thyrididae.** Allied to *Pyralidae* but with two anal nervures in hind-wing and no maxillary palp. A small family of smallish moths, mostly tropical.

Fam. 35. **Lasiocampidae.** Antenna bipectinate in both sexes. No first maxillae and no frenulum. The Eggar-moths are very hairy and often of a brown colour, with considerable sexual dimorphism. The eggs are smooth and sometimes concealed by hairs deposited by the parent. The larvae are remarkably hairy. The pupa is enclosed in a compact, hard cocoon. The family includes some hundred genera with five times as many species. It occurs all over the world except in New Zealand. *Lasiocampa*, *Odonestis*, *Erio aster*, *Poecilocampa* and *Trichiura* are British.

Fam. 36. **Endromidae.** Imago strong and large, flying by day in birch-woods. The caterpillar is said to bend back the anterior segments over the posterior somewhat as does a saw-fly larva. *Endromis* is endemic in Great Britain; *E. versicolor* the "Kentish glory" constitutes the family.

Fam. 37. **Pterothysanidae.** The posterior border of the hind-wing bears long hairs. No frenulum. A black and white Indian genus *Pterothysanus* constitutes the family.

Fam. 38. **Lymantriidae.*** Antennae bipectinate in males only. Frenulum very rarely absent. Sub-costal nervure diverges about the middle of the cell and connects with the first radial. First maxillae reduced. Smallish insects of silver white or sombre coloration known as Tussock-moths. Larvae with highly coloured tufts of hair. The cocoon, and even the pupae are often hairy. The female imago is often wingless, or its wings are small and it does not fly. The tip of the abdomen often bears a thick tuft of hairs. *Psilura monacha*, the "Nonne" of the Germans, is terribly destructive to forest trees in Central Europe, especially to conifers, on which the larvae feed. *Porthetria dispar* is the "Gipsy Moth," the introduction of which into Massachusetts has been a source of great trouble and expense to the government of the United States. The family is large, with nearly two hundred genera and eight hundred species, and is very widely distributed. *Porthesia* (*Liparis*), *Leucoma*, *Laelia*, *Ocneria*, *Psilura*, *Dasychira* and *Orgyia* are British genera.

Fam. 39. **Hypsiidae.** The nervures resemble those of the preceding family; but the first maxillae are well developed and the labial palps are long and turned up. Yellow and grey moths from the warmer regions of the Eastern hemisphere.

Fam. 40. **Arctiidae.** The sub-costal nervure coalesces with the radial and so seems to emerge from the middle of the cell. Frenulum present. The Tiger and Ermine-moths form an enormous family with five hundred genera and three thousand species, cosmopolitan in distribution. The larvae are often hairy, and the imagos usually brightly coloured and showing a high degree of sexual dimorphism. Some of them are remarkable amongst moths for the sounds they produce. *Nycteola* (*Sarrothripus*), *Earias*, *Halias* (*Hylophila*), *Nola*, *Nudaria*, *Setina*, *Calligenia*, *Lithosia*, etc., are British.

Fam. 41. **Agaristidae.** Antennae usually clubbed and hooked. The wing nervures of the Noctuid type (see below). A varied collection of usually diurnal, sometimes crepuscular, moths with bright wings; absent from Europe, but numerous throughout the warmer regions of Africa, Australia, Asia and North America.

Fam. 42. **Geometridae.** Delicate moths with large wings. The second median nervure of the fore-wing is usually closer to the first than to the third. The sub-costal nervure of the hind-wing diverges beyond the cell, with which it may fuse. Tarsi long, not hairy. The "Carpets or Pugs" form a very large family, with very characteristic larvae known as "Loopers" or Geometers. In repose the larvae hold on by the two posterior pairs of pro-legs; all the anterior parts of the body frequently projecting rigid and twig-like, supported by a thread extending from the mouth to some point near at hand. The male usually has remarkable antennae. Some species have wingless females or females with

* Often termed Liparidae.

wings much reduced. The elongated larvae have lost the anterior four pairs of pro-legs, and retain only a pair on the ninth abdominal segment and the anal pair, and as a consequence they "loop" when moving, being apt to assume a position in which the front and hind end of the body is supported whilst the centre rests without support. The cocoons are slight, in many cases absent, the pupa being naked and subterranean. The family is cosmopolitan. *Geometra*, *Nemoria*, *Phorodésma*, *Iodes*, *Hemithea* are amongst the British representatives.

Fam. 43. **Noctuidae**. Sombre moths with proboscis and frenulum. The fourth and fifth radials of the fore-wing arise from the third, and this has a cross-nervure linking it with the second. This is the dominant family of the Heterocera, with some eight thousand species. As the name implies they are night-flyers, and they are provided with complicated organs at the base of the thorax to which a sensory function has been attributed. The larvae share the nocturnal habits of the perfect insect; usually they have ten pro-legs, but one or two pairs may be wanting. These larvae are the cause of immense damage to crops in America, amongst the more destructive species being the "Army worm" *Leucania unipunctata*, the "Cotton-worm" *Aletia xylinæ*, the "Boll-worm" *Heliothis obsoleta* (*armigera*) and others. The pupae may be naked and buried in the earth or enclosed in a cocoon made of vegetable fragments. The family is cosmopolitan. British genera include *Agrotis*, *Noctua*, *Triphaena*, *Mamestra*, *Hadena*.

Fam. 44. **Epicopeiidae**. Antennae bipectinate in both sexes. The cell in each wing is crossed by a nervure which in the fore-wing is forked. The maxillary palps are very small. The moths of this small family of seven or eight species, all united in the single genus *Epicopeia*, are very like some swallow-tailed butterflies of the Papilionidae. The caterpillars have dermal glands which secrete a snow-white waxy substance. They are rare and live in Java, Japan, China and India.

Fam. 45. **Uraniidae**. No frenulum. The fifth radial of the fore-wing unites with the first median, and in the hind-wing a single anal nervure is usually found. Antennae filiform. A small family of six genera and some sixty species, with large wings often "swallow-tailed." The larvae have ten pro-legs and bear sharp tubercles on each segment. The pupa has its first maxillae prominent and ends in a spine. The family is tropical. *Urania* is one of the most beautiful of the Lepidoptera. Several species have a very curious structure in the abdomen, consisting chiefly of two apertures, one on either side of the second segment, each leading into a large cavity extending almost to the middle line.

Fam. 46. **Epilemidae**. Frenulum present. The sub-costal of the hind-wing is free from the radial, and the fifth radial, of the fore-wing arises as a twig from the first median. The hairy larvae have ten pro-legs. Like the *Uraniidae*, they have a peculiar sense-organ at the base of the abdomen.

Fam. 47. **Pyralidae**. The second median of the fore-wing arises from the cell nearer to the third than to the first; there are two anal nervures in the fore-wing and three in the hind-wing, where the sub-costal approaches or touches the radial. Antennae usually simple, legs often long. The Pyralidae form a very large family of small moths. The proboscis is often very long. The larvae have ten pro-legs with complete circlets of hooks; they are usually naked with a very few scattered hairs, and are unattractive and as a rule concealed in rolled up leaves or vegetable debris; a few are aquatic. The pupae have but two free segments and

are protected by a cocoon. The imagos, which include both day- and night-moths, are plain and often marked by three lines and three spots. The family is cosmopolitan and there are a hundred and fifty British species. Amongst the British genera are, *Pyralis*, *Cledeobia*, *Aglossa*, *Scoparia*, *Nomophila*, *Odontia*, *Pyrausta*, *Rhodaria*, *Herbula*, *Ennychia*, *Crambus*, *Platytes*, *Hydrocampa* and many others.

Fam. 48. **Pterophoridae.** The fore-wing has two, and the hind-wing three deep clefts, which separate the wings into plumes, unknown in other moths, with the exception of the succeeding family. This is a moderate sized family with some thirty British representatives. The larvae are slow and heavy, very hairy; they live exposed on leaves. The pupae have three or four free segments and are covered with hairs or protected by a slight cocoon. The hind-wings are more cleft than the others. *Agdistis*, represented in this country, has its wings entire. The family is widely distributed, and *Cnaemidophorus*, *Platyptilia*, *Amblyptilia*, *Oxyptilus*, *Pterophorus* are amongst the British genera.

Fam. 49. **Alucitidae.*** Each wing cleft almost to the base into six plumes. *Alucita*, the only genus, is represented in Britain by *A. polydactyla*, which feeds on honey-suckle.

Fam. 50. **Tortricidae.** The second anal nervure of hind-wing forked at the base, and a sub-costal is always present. The first maxillae have no palps and the labial palps are blunt. The *Tortricidae* are a very extensive family of small moths whose hind-wings have no pattern. The wings are sometimes slightly fringed, and the front pair may bear metallic spots. The larvae have ten pro-legs; they live within the tissue of the plants on which they feed, or in rolled-up leaves: in either case they cause great injury to trees. The family is widely distributed and represented in this country by the genera *Tortrix*, *Dichelia*, *Amphisa*, *Oenectra*, *Lep-togramma*, *Peronea*, *Rhacodia*, *Teras* and others.

Fam. 51. **Tineidae.** The nervures are arranged as in the preceding family, excepting that the second anal of the hind-wing is not forked. The wings are usually narrow and pointed, and the hind-wing may be fringed. Maxillary palps often present, and labial palps pointed. This is an immense family of small moths with some seven hundred British species. The larvae live exposed on plants, or mine in a great variety of substances such as cloth, the horns of live antelopes, camels' dung, fur, hair and horses' hoofs, potatoes, old wood, corks, etc., etc. In structure these caterpillars vary greatly; they may be altogether devoid of legs; many of them have protective cases. The pupae also show much diversity. One or two species of *Tinea* are viviparous; and *Solenobia*, which is wingless in the female, is at times parthenogenetic. The group is cosmopolitan and represented in Britain by *Diplodoma*, *Scardia*, *Blabophanes*, *Tinea*, *Tineola*, *Lampronia*, *Nemophora* and others. The so-called "clothes moths" belong to this family. *Pronuba synthetica* (Fig. 459) lays her eggs on the Yucca and in so doing fertilizes the flowers.

Fam. 52. **Eriocephalidae.** The mandibles are fairly well developed in the imago. The maxillae have each two lobes, not elongated, and a flexible, five-segmented palp; they form no proboscis. The wings have no frenulum or shoulder, but a small jugum; the front and hind pair probably act independently. A small family which by the foregoing characters and by the large number of cross nervures on the wings shows

* Orneodidae of some writers.

relationship with the Trichoptera. The larva has sixteen pro-legs and lives amongst damp moss. Its head bears long antennae and is retractile into the following segments. The mandibles of the pupa are functional; the pupa is said to bite a hole out of the cocoon, through which the imago frees itself. The imago has bronzy wings. The family is Holarctic, and also represented in New Zealand by *Palaeomicra*. *Eriocephala calthella* is a very common British species, found early in the year on buttercups. By the form of its mouth-parts, *Eriocephala* shows that Lepidoptera can be considered as mandibulate insects, in the majority of which the mandibles are absent or extremely reduced.

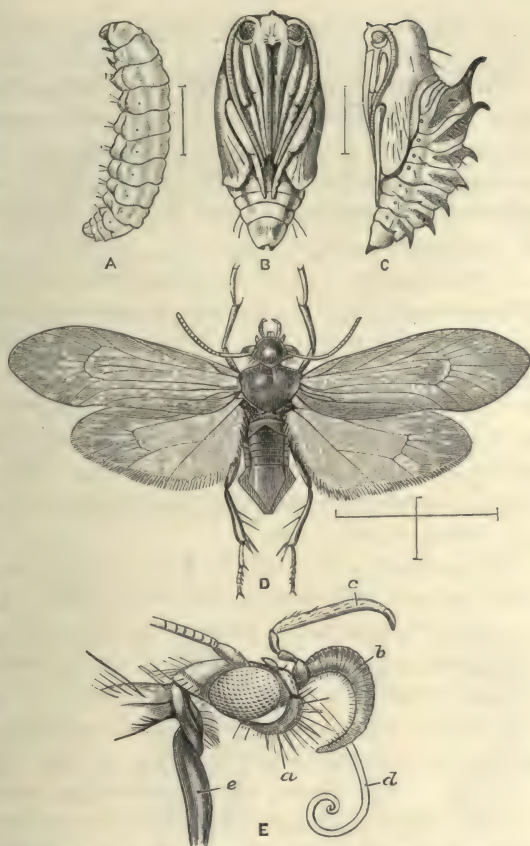


FIG. 459.—*Pronuba synthetica*. North America. A larva; B, C pupa, ventral and lateral aspects; D female moth; E head and part of thorax of the female moth; a labial palp; b maxillary tentacle; c maxillary palp; d proboscis; e base of front leg (after Riley, from Sharp).

Fam. 53. **Micropterygidae**. The cross nervures are numerous, but not so many as in the *Eriocephalidae*, and the sub-median nervure is forked. No frenulum or mandibles are present. Maxillae form a short proboscis with long palps. The family is represented by the genus *Micropteryx*. The female has a cutting ovipositor by means of which she lays her eggs in the mesophyll of a leaf. The larva is without feet; before transformation it makes its way underground, where the pupa surrounds itself with a cocoon strengthened by grains of earth. The pupa, like that of the Trichoptera, has a free head and appendages including large mandibles, but these latter are lost in the imago. The moths are small with a metallic sheen. *Micropteryx* occurs in Northern and Middle Europe including Britain.

Order 19. COLEOPTERA.*

The anterior wings, called elytra, are hard, and when at rest they cover in the functional hind-wings and come together closely with a straight median juncture ; mouth-parts biting, with stout mandibles ; second maxillae much fused to form an effective lower lip. Metamorphosis complete ; larva grub-like ; pupa soft and exhibiting the parts of the imago.

The Coleoptera form a very large Order with some hundred and fifty thousand described species. Almost any member of the Order may easily be recognized by the straight suture which in the great majority of cases lies between the hard, leathery elytra, or fore-wings, when they are at rest. The hind-wings alone are used for flight, and the group on the whole is less given to flying than the other large Orders of Insects. The head bears antennae, whose segments vary in number from one to thirteen, and biting mouth-parts.

The prothorax is usually mobile ; the pronotum, and the elytra when at rest, effectively cover in the body ; a small triangular area of the mesonotum, situate at the base of the elytra and termed the scutellum, being frequently the only other part of the dorsal surface visible ; in many cases, however, the elytra are short, and leave some dorsal abdominal segments exposed. The sterna are usually clearly defined, as are the episterna and epimera. The bases of the hind-legs cover part of the anterior abdominal segments, of which usually but five are distinguishable ventrally, though seven or eight appear dorsally. One or more segments are tucked into a genital bursa at the posterior end of the body.

The elytra are very rarely absent and then only in the female sex ; but the hind-wings are not unfrequently diminished to the smallest proportions, and in these cases the right and left fore-wings are frequently soldered together. The elytra are often ornamented with ridges and depressions. The hind-wings alone are membranous ; they have but few cross-nervures.

* Strauss-Durckheim, *Monograph*, Paris, 1828. Horn, *Revision der Cicindeliden*, Berlin, 1898. Régimbart, *Ann. Soc. Ent. France*, 1882-3 and 1886. Raffray, *Rev. Ent. franc.*, ix, 1890. Ganglbauer, *Die Käfer von Mitteleuropa*, Vienna, in progress. Perris, *Larves de Coléoptères*, 1898. Newport, *Tr. Linn. Soc.*, xx, 1851. Lacordaire, *Genera des Coléoptères* (Suites à Buffon), x, Paris, 1874. Mulsant, *Coléoptères de France*.

The mandibles are well developed; the first maxillae have each two well-marked lobes and a palp; the second maxillae are somewhat reduced, with a well-formed palp, and are very completely fused to form a labium. The legs are usually well developed, and the tarsi may have from one to five segments, a detail of great systematic import. The metamorphosis is complete. The larvae are as a rule grub-like, but they vary greatly, from well-marked campodeiform active creatures to legless grubs. As a rule a head, three thoracic segments with or without legs, and nine abdominal segments are patent, but in many cases the abdomen presents ten segments. When exposed the larvae may have a hard and coloured integument, but those which lead a hidden life are usually white and soft.

The pupa usually is hidden in the earth or concealed near the larval food. It is, as a rule, an unpleasant, whitish-looking, soft object with all its appendages projecting, but some families have obtected pupae whose limbs are fused to the body. In many, a cocoon of some extraneous material, is formed, and as a rule the period passed in the pupal stadium is short and does not surpass a very few weeks.

There is a long oesophagus, and in the carnivorous beetles a well-developed muscular proventriculus. As a rule the number of malpighian tubules is four

or six. The central nervous system varies in its degree of concentration. The ovarian tubules are many on each side, with very numerous ova; the male possesses a penis which is usually retracted into the abdomen.

Anobium, the so-called "death-watch," produces its sounds by a tapping movement. Longicorn beetles make a sharp sound by rubbing the scutellum against the edge of the pro-

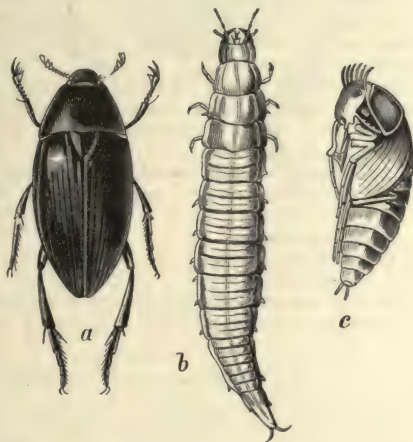


FIG. 460.—*Hydrophilus piceus*. a beetle; b larva; c pupa.

thoracic cavity, *Necrophorus* and Weevils chirp by rubbing the abdomen against the hinder end of the elytra.

In order to cope with the large amount of material presented to the systematist by this enormous order, it has been divided into six sub-orders, five of which are well characterized, while the sixth (i.e. the Polymorpha) consists of those beetles which do not fall into line with any of the other five. This is obviously not a natural system; convenience and insufficient knowledge alone excuse it. It is used here; but the following note on a proposed new scheme is also given:—

L. Ganglbauer (München. Koleop. Zeitschr., I, pp. 271-319) has proposed a new classification of Coleoptera, depending largely on the nervuration of the (metathoracic) wings. Of these wings there are three main types: (i) the *Adephaga* type, characterised by certain cross-veins; (ii) the *Staphylinoidea* type, without cross-veins; and (iii) the *Malacoderm* type, chiefly characterised by the presence of a 2-pronged fork with the prongs directed towards the base of the wing, formed by confluence of two branches of the median vein. The ADEPHAGA are further divided from all other Coleoptera as a distinct sub-order. The outline of the classification is as follows:—

Sub-order I. ADEPHAGA, chiefly characterised by the wings of the first type, simple tubular testes, and the two-jointed tarsi of the primitive campodeiform larvae.

Sub-order II. POLYPHAGA. All other Coleoptera. Wings of second or third type. Testes more complicated. Larvae very various, often legless, and never with two-jointed tarsi. This sub-order is further divided into six series:—

- | | |
|-----------------------------|--|
| (i) <i>Staphylinoidea</i> | } together very nearly corresponding to the <i>Poly-</i> |
| (ii) <i>Diversicornia</i> | |
| (iii) <i>Heteromera</i> . | |
| (iv) <i>Phytophaga</i> . | |
| (v) <i>Rhynchophora</i> . | |
| (vi) <i>Lamellicornia</i> . | |

It is thus seen that Ganglbauer considers the *Lamellicornia* the highest-developed, and the *Adephaga* decidedly the most primitive, Coleoptera.

Sub-order 1. LAMELLICORNIA.

Tarsi with five segments. The distal segments of the antennae to the number of three or more are flattened on one side and leaf-like. When at rest these leaf-like segments lie touching one another and cause the antennae to appear clubbed; but they can be opened out.

The larvae of this sub-order have three pairs of thoracic legs, and their body is somewhat curled and swollen posteriorly. They live underground and eat decaying vegetable matter such as roots and dung. Some of them stridulate. In the imago the nervous system is very concentrated, in some genera there being, behind the oesophagus, but one ganglion.

Fam. 1. **Passalidae**. Elytra conceal abdomen. Large and movable labrum. Antennae curled when at rest, and their lamellae then touch one another. Five abdominal sterna visible.

Large black beetles found in tropical forests. The third pair of larval legs modified to form a very small toothed stump which plays over a

grating on second legs and produces a sound. The family contains several hundred species but is unrepresented in Europe and almost so in North America.

Fam. 2. **Lucanidae.** Elytra conceal abdomen. Antennae elbowed and with little co-adaptation of terminal joints. Labrum fixed and small. Five abdominal sterna visible. This family includes the Stag-beetles, remarkable for the great enlargement of their mandibles in the males. The legs are long, and the fifth or last of the tarsal segments is much larger than the others. The larvae are fat, white grubs with thick chitinous head armature, which live in the wood of trees. The family with some 600 species is best represented in the Malay district and in the temperate regions of Europe and Asia. *Lucanus cervus* is the British stag-beetle.

Fam. 3. **Scarabaeidae.** Elytra leave hind end of abdomen uncovered. Antennae with highly developed leaflets. Six abdominal sterna visible. A very large family of some 13,000 species, known familiarly as chafers. The larvae are white and stout and usually curved, and end in a swollen portion termed the "sac." The body of these grubs shows transverse wrinkling. Many feed on roots and underground stems and others on dung. The imagos often eat leaves. The family is cosmopolitan but most numerous in the warmer parts of the earth. *Scarabaeus sacer* is probably the sacred beetle of the Egyptians. *Melolontha vulgaris*, the cockchafer, is one of the most destructive beetles to growing crops. *Cetonia*, the rose-chaffer.

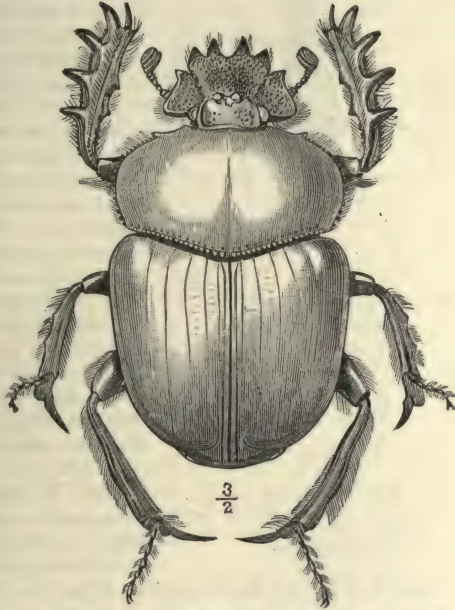


FIG. 461.—*Scarabaeus sacer*. Portugal. From Sharp.

Sub-order 2. **ADEPHAGA or CARABOIDEA.**

Tarsi with five segments. Antennae filiform. Outer lobe of maxilla very often divided into a two-jointed palp (the ordinary maxillary palp also being present). Usually five abdominal terga and sterna visible, and six pleura.

This sub-order includes six families of ground- and tiger- and water-beetles. The larvae are usually active and have well formed legs with two tarsal segments.

Fam. 4. **Cicindelidae.** Antennae eleven segmented. Clypeus reaches laterally beyond the insertion of antennae. Outer lobe of maxilla forming a two-segmented palp. The inner lobe of the maxilla ends

in an articulated hook. The beetles of this family, known as the Tiger-beetles, are active, predaceous Coleoptera feeding on small insects which they run down. The larvae live in the ground, but,

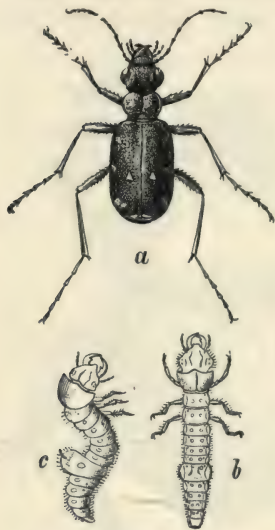


FIG. 462.—a *Cicindela campestris*. b, c its larva with the two dorsal hooks on the fifth abdominal segment.

protruding their head, capture with lightning rapidity any insect which comes within range. The family, which contains some 1,400 species, is cosmopolitan but mostly met with in the tropics. *Cicindela*, the British tiger-beetle, has five species in our country (Fig. 462).

Fam. 5. **Carabidae**. Differ from the preceding in that the clypeus is narrower and the inner lobe of the maxilla has the hook not articulated. Antennae pubescent. Hind legs not markedly different from the middle pair. The ground beetles comprise about as many species as the *Scarabaeidae*. The larvae are campodeiform and active, with large nipper-like mandibles; both they and the imago are as a rule carnivorous, and devour insects, worms and snails. A few have the wings rudimentary, and those which dwell in caves are often blind, e.g. *Anophthalmus*. *Carabus*, *Bembidium*, and *Harpalus* are British genera. *Pterostichus* (Fig. 378).

Fam. 6. **Amphizoidae**. Antennae not pubescent, outer lobe of maxilla without a joint. Hind legs modified for swimming.

This family has but a single genus *Amphizoa* found in both larval and imaginal stages in swift streams clinging to stones, etc.

Fam. 7. **Pelobiidae**. Antennae not pubescent, outer lobe of maxilla jointed. Hind legs adapted for swimming. Tarsi longer than tibiae. This family has also but one genus *Pelobius* found in Britain, South Europe, Tibet and Australia. The larva has a superficial resemblance to a gigantic zoea; it breathes by branchial processes. The imago has powerful stridulating organs.

Fam. 8. **Haliplidae**. Antennae ten-segmented, not pubescent. Metasternum has a transverse suture. The coxae of hind legs form plates which project under the abdomen and cover their femora. Small oval aquatic beetles whose larvae bear a number of fleshy processes, which may be respiratory as in *Cnemidotus*. There are but three genera, all British, with a hundred species. *Haliplus* is cosmopolitan.

Fam. 9. **Dytiscidae**. Antennae with eleven segments, not pubescent. Hind legs capable of swimming only. Outer lobe of maxilla forms a two-segmented palp. Metasternum has no transverse suture. A moderate sized family of carnivorous water-beetles most abundant in the colder regions. The larvae are active and ferocious creatures sucking up the juices of their prey through hollow mandibles. The imagoes carry a supply of air under the elytra. Many of the males have a peculiar pad or sucker on their fore-feet, by which they adhere to the female. *Dytiscus*, *Cybister*, *Hydroporus*, etc.

Sub-order 3. POLYMORPHA.

Antennae usually clubbed or toothed on inner border. This a loosely defined sub-order of some fifty families of very varying importance.

Fam. 10. **Paussidae.** Antennae usually with two segments. Long elytra but not covering end of abdomen. Tarsi with five joints. Small beetles of very bizarre appearance frequenting ant's nests. They seem to be popular with the ants, whose larvae and eggs they eat, but the reason of their popularity is not very apparent. *Pausseus*.

Fam. 11. **Gyrinidae.** Antennae short. Meso- and meta-thoracic legs adapted for swimming. Each eye divided into two. These beetles are termed whirligigs from the mazy dance they perform on the surface of the water. They are emphatically surface dwellers, and if they dive they soon ascend again. The larvae are long, and the nine abdominal segments bear each two feathered branchiae. Both larvae and imagos are carnivorous. *Gyrinus*, with eight British species, and a single species of the nocturnal *Orectochilus*, represent the family in this country.

Fam. 12. **Hydrophilidae.** Antennae with less than eleven segments, sub-divided into three regions. Palps of first maxilla often longer than antennae. Five visible segments in abdomen. A cosmopolitan, large family mostly aquatic. *Hydrophilus piceus* (Fig. 460), British, carries a layer of air, renewed by the action of the antennae, entangled in hairy patches beneath the body; among these patches the tracheae open. Egg-cocoons are unusual amongst Coleoptera, but many members of this family construct them. *Spercheus*, British, carries its cocoons beneath its abdomen. The larvae are carnivorous and as a rule aquatic.

Fam. 13. **Platypyllidae.** Wingless. Antennae with three segments, the last of which is sunk in the second; both second and third bear long setae. The mentum is trilobed posteriorly. This family consists of a single species, *Platypyllus castoris*, which lives and lays its eggs amongst the hair of the Beaver in both the old and new world.

Fam. 14. **Leptinidae.** Antennae with eleven joints, thickening towards tip. Eyes absent or imperfect. Five tarsal segments. Elytra conceal abdomen. Two genera, *Leptinillus* which like *Platypyllus* lives on beavers, and *Leptinus* which lives on mice and in the nests of humble-bees, each with a single species, constitute this family. The latter genus is British (Fig. 463).

Fam. 15. **Silphidae.** Straight, clubbed antennae, usually eleven-segmented. Tarsi usually five-segmented. Abdominal segments usually five or four, rarely seven, visible, but the anterior three terga at least are membranous. The Carrion-beetles form a large cosmopolitan family, very varying in size. The well-known burying beetles by making tunnels under small dead mammals and birds, succeed in interring them, and then devour them in peace. Many species dwelling in caves are sightless. Others live amongst moss or under bark. The larvae are active with



FIG. 463.—*Leptinus testaceus*.
Britain. From Sharp.

well developed terga, and somewhat resemble wood-lice. Those of *Silpha* run about in search of carrion.

Fam. 16. **Scydmaenidae**. Minute. Five-segmented tarsi. Six visible abdominal segments. Elytra cover, or almost cover, abdomen. A cosmopolitan family of very small black or brown beetles living amongst moss, under bark or stones, and in ants' nests. They feed on mites.

Fam. 17. **Gnostidae**. Minute. Five-segmented tarsi, three segmented antennae. Elytra conceal abdomen which has apparently but three segments; the apparent first however consists of three fused plates. Two species found in ants' nests in South America constitute this family.

Fam. 18. **Pselaphidae**. Minute. Elytra shortened so as to cover at most half the abdomen. Maxillary palps large. Abdominal segments rigid. Tarsi three-segmented. A large family of peculiar beetles; most found only in ants' nests. They produce from pubescent tufts some secretion which the ants eat, and in return, at least in some cases, the ants feed them. *Claviger* has been seen to eat the ant larvae.

Fam. 19. **Staphylinidae**. Elytra shortened so as usually to cover but two of the abdominal segments. Ten abdominal terga visible, and these are hardened, and the segments very mobile. Three to five tarsal segments. An enormous cosmopolitan family with some nine thousand species known as Rove-beetles or "Devil's coach-horses." The metathoracic wings, like those of the earwigs, are often extensive and tucked away under the minute elytra. The beetles often fly well. They are usually long and narrow, and very active; they live on carrion, snails, worms, other insects, fungi, etc. A few species live in ants' nests. The larvae are active and campodeiform; their feet are terminated by a single claw. The pupae of some are obteated, that is ensheathed in a hardened exudation which fastens all the appendages together. *Ocypus* and many others British.

Fam. 20. **Sphaeriidae**. Minute. Eleven-segmented, clubbed antennae. Three-segmented tarsi. Three visible abdominal sterna. Very small beetles with but three or four species mostly found on mud. *Sphaerius acaroides* occurs in the fens of Cambridgeshire.

Fam. 21. **Trichopterygidae**. The smallest members of the Order. Antennae slender, their apical joints thickened. Tarsi with three segments. Wings narrow and long, fringed with hairs. A widely distributed family whose members live amongst moss and leaves. They are all very minute and the smallest forms are the smallest of Insects. *Nanosella fungi* measures but one-hundredth of an inch in length. There are some eighty British species.

Fam. 22. **Hydroscaphidae**. Very tiny, aquatic beetles with long abdomens. Antennae have eight segments. Only a few American and South European species known.

Fam. 23. **Corylophidae**. Minute with fringed short wings. Tarsi with four segments but only three easily visible. A widely distributed but small family of minute beetles, some of which live in thatches.

Fam. 24. **Scaphidiidae**. Front coxae conical, hind coxae widely separated. Prothorax closely applied to the succeeding segments. Five segments to the tarsi. This family is small and widely distributed, with very active members which live among fungi. *Scaphidium* is British.

Fam. 25. **Synteliidae**. Antennae clubbed. Front coxae transverse. Labium prominent. Five visible abdominal sterna and eight or nine terga. A widely distributed family of only five species which feed on sap exuding from plants.

Fam. 26. **Histeridae**. Compact, hard, beetles. Antennae short, elbowed and clubbed. Elytra very frequently with clear-cut striae, cut off behind, leaving two abdominal terga exposed. Tarsi with five segments. This is a moderate-sized family, the members of which are found in dung, carcasses, or amongst decaying vegetation, and in ant-heaps. The larvae are elongate, soft, but with well-developed mandibles and short legs. Both larvae and imago are said to live on Dipterous and other maggots.

Fam. 27. **Phalacridae**. Compact beetles. Elytra cover abdomen. Antennae slightly clubbed, with eleven segments. Pronotum as broad as base of elytra, and overhanging the head. A small widely distributed family of small beetles. The larvae frequent the inflorescences of Composites and pupate in earthen cocoons.

Fam. 28. **Nitidulidae**. Antennae with eleven segments the last three of which form a club. The coxae of all the legs separated, and each with an outer prolongation. Tarsi with five segments, the fourth small. A moderately large and diverse assemblage of small beetles which inhabit flowers, vegetable refuse and carcasses. Some live under bark, eating the larvae of wood-boring insects. The genera *Meligethes* and *Epuraea* are abundant in Britain and some of the former injure rape crops.

Fam. 29. **Trogositidae**. Antennae with an asymmetrical club. Five-segmented tarsi, the first segment much reduced. Coxae of metathoracic legs in contact. A small but widely distributed family with predaceous larvae that feed on other insect larvae. They live under bark, amongst corn, etc. *Trogosita* is cosmopolitan.

Fam. 30. **Colydiidae**. Antennae short and clubbed. Tarsi with four segments. Pro- and meso-thoracic coxae round and sunk in body. Five visible abdominal sterna with little mobility. The members of this family lodge in the cracks of the bark of moss-grown trees, often leading very sedentary lives; many are said to be disappearing with the destruction of the primeval forests. *Bitoma* is British.

Fam. 31. **Rhysodidae**. Tarsi with four segments. A large mentum hides the mouth-parts. Front tibia notched. A very small family found mostly in the tropics and sub-tropics.

Fam. 32. **Cucujidae**. Antennae eleven-segmented, rarely clubbed. Pronotum often toothed laterally. Tarsi with four or five segments. Anterior and middle coxae globular and imbedded. A large family of insects of somewhat flattened, oblong shape, usually found under bark. *Silvanus surinamensis* however lives amongst grain. They are most abundant in warm climates.

Fam. 33. **Cryptophagidae**. Differ from the preceding in having large terminal segments to their antennae. Tarsi five-segmented, but a few species have only four segments in the posterior legs of the male. A small family of minute beetles said to eat mould; they live all over the world but are more numerous in temperate than in hot climates. They usually frequent vegetable debris, but the larvae of *Antherophagus* lives in humble-bee nests, and those of *Cryptophagus* in the nests of wasps.

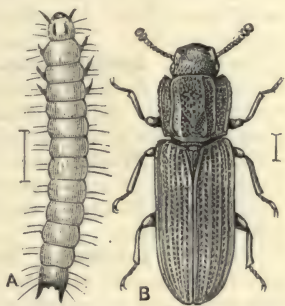


FIG. 464.—*Bitoma crenata* (Colydiidae) Britain. A larva (after Perris); B perfect insect.

Fam. 34. **Helotidae**. Anterior and middle coxal cavities round, coxae wide apart. This family is allied to the *Nitidulidae* but differs in the structure of the coxae. There is but one genus, found in Japan, the Malay peninsula and East Africa.

Fam. 35. **Thorictidae**. Antennae short, clubbed. Front coxae small and not transverse, metasternum very short. Tarsi with five segments. Only one genus *Thorictus* found in Ants' nests around the Mediterranean.

Fam. 36. **Erotylidae**. Tarsi apparently four-segmented with the first three joints broad and pubescent; there is however a minute fifth segment. Antennae clubbed. Coxal cavities round. The family is large, mainly found in hot climates; the members of it feed on fungi. *Tritoma* is British.

Fam. 37. **Mycetophagidae**. Tarsi slender, all four-segmented, except in the males where only three segments are found in the anterior limbs. Coxae oval not imbedded. Small beetles often with red or yellow dots, found amongst fungi, especially such fungi as attack timber. Widely distributed. *Litargus* is British.

Fam. 38. **Coccinellidae**. Four-segmented tarsi, but only three segments visible easily as the third is sunk in the second; first and second pubescent. Antennae short and clubbed. Pronotum largely concealing head. The lady-birds, *Coccinella*, are a largish family of some 2,000 species. The larvae are oval with tubercles bearing hairs; they devour plant-lice and scale-insects, etc. The beetles are rounded or oval and often brightly ornamented.

Fam. 39. **Endomychidae**. Tarsi really four but apparently three-segmented as in the *Coccinellidae*; but the clubbed antennae and the legs are longer. An exotic family with few representatives in cold climates. They live on plants especially cryptogams.

Fam. 40. **Mycetaeidae**. Four-segmented tarsi usually slender. Anterior and middle coxae globular. A small family of small fungus-eating insects found chiefly in the Holarctic region. *Mycetaea hirta* is common in London cellars.

Fam. 41. **Latridiidae**. Three-segmented tarsi, front coxal acetabula round. Pronotum usually narrower than elytra. Minute but widely distributed and very numerous beetles, with weakly developed mandibles. The larvae are soft, oval in outline, and bear hairs. They live in vegetable debris and eat fungi. *Latridius* is British.

Fam. 42. **Adimeridae**. Four-segmented tarsi, but as the second and third segments are concealed between the fourth and the broad basil joint, they are apparently only two segmented. This family contains but one genus, the American *Adimerus*.

Fam. 43. **Dermestidae**. Five-segmented tarsi. Eleven-segmented, clubbed antennae which can be tucked into a groove under the pronotum. A smallish family of cosmopolitan beetles, many of which live on plants, while others e.g. *Dermestes vulpinus* devour skins. Their larvae mostly live on dried animal matter and *Anthrenus museorum** is often very destructive in zoological Museums. They are ornamented with dense tufts of hairs, and pupate in their cast larval skin. They seem capable of living without water though their bodies contain as high a percentage of water as other insect larvae.

Fam. 44. **Byrrhidae**. Five-segmented tarsi. Legs short: the tarsi

* A. J. Ewart, *J. Linn. Soc. London (Zool.)*, xxx, 1907, p. 1.

can be folded back into grooves on the tibiae, and all the legs closely pressed against the body. These Pill-beetles are round and very convex. They live amongst moss, or in running water, etc., and feed on sap. The larvae are soft except for the prothorax and last two abdominal segments which are strongly chitinized. The Pill-beetle *Byrrhus pilula* is common in Britain. The family is small and cosmopolitan.

Fam. 45. **Cyathoceridae**. Tarsi not segmented. Antennae four-segmented. The only species of this family is the Central American *Cyathocerus horni*, a minute, broad beetle.

Fam. 46. **Georyssidae**. Tarsi four-segmented. Antennae clubbed and short. Prosternum small. Front coxae exerted but separated. Minute beetles of which only some twenty-five species are known. *Georyssus* is British; it lives in wet places and covers itself with mud.

Fam. 47. **Heteroceridae**. Eleven-segmented short antennae with the last seven segments broad and forming a toothed club. Four-segmented tarsi. Legs adapted for digging. This family has but one genus, *Heterocerus*. It lives in burrows on the edges of ponds and streams. By rubbing their third pair of femora on the first abdominal sternum the beetles produce a shrill noise. They are most abundant in the northern temperate zone. Seven species are British.

Fam. 48. **Parnidae**. Five-segmented tarsi, last segment elongate. Head usually hidden beneath pronotum. The prosternum projects backward and is received into a groove on the mesosternum. Not a large family of small, aquatic beetles found all over the world. *Parnus* is European, *Paephenus* American.

Fam. 49. **Derodontidae**. Five-segmented tarsi, fourth segment slender and small. Anterior coxae prominent and transversely extended. A family of very few species divided between the genera *Dero-dontus* and *Peltasticta* of the Holarctic Region.

Fam. 50. **Cioidae**. Four-segmented tarsi. Antennae clubbed, short. Anterior and middle coxae small and deeply embedded. Small or minute beetles which browse on fungi, especially on those infesting timber. *Cis*.

Fam. 51. **Sphindidae**. Tarsi five-segmented. In other respects this family resembles the *Cioidae*, and like its members these beetles live on fungi which attack timber. *Sphindus* and *Aspidiphorus* are British.

Fam. 52. **Bostrichidae**. Tarsi five-segmented, the first segment very short. Anterior coxae conspicuous but not in contact. The beetles of this family live in wood and do much damage in forests. The larvae have a swollen thorax and the end of the abdomen is turned forward ventrally.

Fam. 53. **Ptinidae**. Tarsi five-segmented, first segment often larger than second. Anterior coxae small. Pronotum covers head, prosternum short. This is a large family of small oblong beetles with thick integuments. They live in organic matter: the "death-watch," *Anobium striatum* (p. 723) bores in furniture both as a larva and as an imago. As a rule the beetle present in "weevily" biscuits is *A. paniceum* (Fig. 465), and others bore in books, compressed meat, opium, etc. The larvae are curved, white grubs like miniature cock-chaffer larvae. The family is widely distributed.



FIG. 465. "Biscuit-weevil." *Anobium paniceum*. From Sharp.

Fam. 54. **Malacodermidae**. Elongate, soft skinned beetles with seven or eight free abdominal sterna. This is a large and varied family of moderate sized beetles. The antennae are often serrated, the tarsi five-segmented. The larvae vary greatly and are predaceous and carnivorous. This family includes the glow-worms *Lampyris noctiluca*, *Luciola italica*, etc.

Fam. 55. **Melyridae**. Antennae serrated or filiform. Six abdominal sterna visible. The *Melyridae* are soft-skinned beetles that frequent flowers, but the larvae are carnivorous. *Malachius*, which gives an alternative name *Malachidae* to the family, has British representatives.

Fam. 56. **Cleridae**. Tarsi five-segmented, but the proximal segment of the hind tarsus very indistinct. Thorax narrower than elytra, head conspicuous. Antennae often clubbed, seldom serrated. Five or six visible abdominal sterna. A varied family of soft beetles often brightly coloured. They are predaceous. The larvae are hairy and brown or red; they feed on other insects notably on Dipterous and Hymenopterous larvae which they find amongst carrion or vegetation. *Tillus*, *Laricobius*, *Cylidrus*.

Fam. 57. **Lymexylonidae**. Tarsi five-segmented. Anterior and middle coxae placed longitudinally. Antennae short and serrated. A small family of under two score species of soft, longish beetles which bore in hard wood. The larvae of *Lymexylon navale* were very destructive in the time of wooden ships. That species and *Hylecoetus dermestoides* are British.

Fam. 58. **Daseillidae**. Antennae serrate or filiform, arising close in front of eyes. Anterior coxae inserted apart, posterior close together. Five visible abdominal sterna. A widely distributed family of smallish beetles. The larvae of some, e.g. the British *Hydrocyphon*, are aquatic, of others subterranean.

Fam. 59. **Rhipiceridae**. Five-segmented tarsi with a hairy, chitinous process between the claws. The male antennae bear long processes. Mandibles strongly incurved. A small, chiefly tropical family. The cylindrical larvae sometimes live in timber. *Rhipicera*, *Callirhipis*.

Fam. 60. **Elaferidae**. Antennae serrate as a rule or pectinate. Posterior angles of prothorax conspicuous. Five visible abdominal segments. The click-beetles form a large family capable, when they fall on their backs, of jumping into the air and so righting themselves. This they do by suddenly forcing a prosternal process into a mesosternal hollow or "catch." The articulation between the pro- and meso-thorax is a loose one. The larvae of the skip-jack beetle *Agriotes lineatus*, sometimes termed the wire-worm, but not to be confused with the Myriapod *Julus terrestris*, causes much damage to crops by gnawing roots. The fire-flies of the tropics, notably the genus *Pyrophorus*, belong to this family, which is large and cosmopolitan.

Fam. 61. **Buprestidae**. Antennae short and serrated. Head partly hidden by pronotum. Prostern projects into a mesosternal depression. Five visible abdominal sterna. A large family of beetles which feed under bark or in timber mostly in hot climates. Often highly ornamented and metallic, so that the elytra are used as decorations. The larvae usually have a very broad and flattened thorax.

Sub-order 4. HETEROMERA

Five tarsal segments on first and second pairs of legs, four on the third.

Fam. 62. **Aegialitidae**. Coxae widely separate. Five abdominal

sterna and the tip of the sixth visible. This family comprises two small and rare beetles from North America.

Fam. 63. **Anthicidae.** Head with an abrupt narrow neck. Base of elytra wider than prothorax. Antennae filiform. A numerous and cosmopolitan family of small beetles which either live in dead wood or frequent sandy and earthy spots.

Fam. 64. **Cantharidae.*** Head narrow behind eyes. Base of elytra narrower than prothorax. Each tarsal claw has an appendage. The oil- and blister-beetles are of fair size and form a large family. They often contain some irritant which raises blisters when applied to the skin, e.g. *Lytta vesicatoria*, the Spanish-fly. The larvae, in many cases (Fig. 467), are at first active and campodeiform, but later inert, motionless and maggot-like; just before pupating, however, they again become active, though they take no food. *Sitaris humeralis*, British, infests in the larval stages the nests of the bee *Anthophora* and devours first the egg of the bee and then the honey stored up as food for the bee larvae.

Fam. 65. **Cistelidae.** Allied to the Tenebrionidae. With pectinated claws. Anterior coxal cavities closed behind. The *Cistelidae* are a cosmopolitan family of moderate size. The larvae are said to eat dead wood.

Fam. 66. **Lagriidae.** Antennae filiform. Anterior coxal cavities closed. Claws smooth. These beetles are hairy and the larvae often have tufts of hairs; the latter are found on leaves. The family is very moderate in size and widely distributed especially in warm countries. *Lagria hirta* is the solitary British representative.

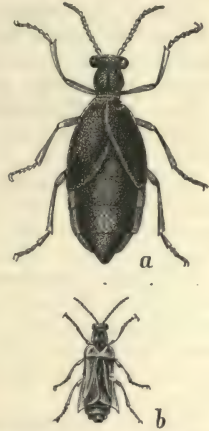


FIG. 466.—a *Meloe violaceus*; b *Sitaris humeralis*.

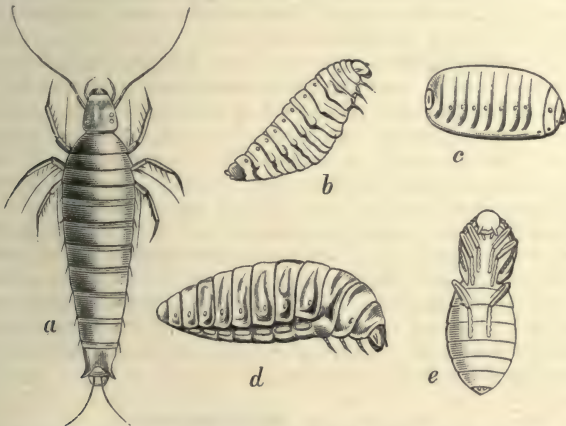


FIG. 467.—Metamorphosis of *Sitaris humeralis* (after Fabre). a First larval form; b second larval form; c pseudo-pupa; d third larval form; e pupa.

* Meloidae of some authorities.

Fam. 67. **Melandryidae**. Anterior coxal cavities open behind. Claws smooth. Head partly hidden by pronotum, not constricted behind. A smallish family of beetles widely distributed in temperate climes. The larvae are cylindrical, with head, thorax and posterior segment chitinous, the rest of the body soft. *Melandrya*, etc., are British.

Family 68. **Mordellidae**. Antennae filiform, slightly serrated. Head constricted behind the eyes, and easily bent down on to the prosternum. Anterior coxae small and spherical. Body convex. A family of active beetles, found often amongst flowers. *Mordella*, *Anaspis*.

Fam. 69. **Monommidae**. Small, oval beetles whose parts are capable of being packed together in a very small compass. A small family unknown in Europe.

Fam. 70. **Nilionidae**. Broad, rounded forms with extensive inflected portions of the elytra. Anterior coxal cavities closed, though they appear open because the tips of the epimera are free. A small, chiefly South American family, found amongst fungi.

Fam. 71. **Oedemeridae**. Antennae long and filiform. Prothorax rounded at the edge. Head not constricted into a neck. A largish, cosmopolitan family of rather soft-skinned, brightly-coloured beetles living in flowers; the larvae live in old wood. The larva of *Nacerdes melanura* lives in timber east ashore on our coasts or river sides. *Asclera* is also British.

Fam. 72. **Othniidae**. Soft insects, with the abdominal segments semi-membranous posteriorly and very mobile. Antennae clubbed. A very small family of doubtful value. *Othnius*.

Fam. 73. **Pyrochroidae**. Head constricted behind and carried horizontally. Antennae strongly serrated or pectinated. A small family of usually red, weak beetles, which however fly actively. They are represented in Britain by *Pyrochroa* sp., the "Cardinal beetles."

Fam. 74. **Pythidae**. Separated from the Melandryidae by the shape of the pronotum, which is oval or heart-shaped and narrower than the base of the elytra. A small family of bark and timber haunting beetles, widely distributed in temperate climates. The very flat larva of *Pytho depressus* lives under the bark of British conifers.

Fam. 75. **Rhipiphoridae**. Resemble the Mordellidae but have large conical anterior coxae. Antennae pectinate in males, serrate in females. A widely distributed family represented in Britain by *Metoeus paradoxus* whose larva preys on wasps' larvae.

Fam. 76. **Tenebrionidae**. Antennae thickening at ends. Front coxae small and spherical, their cavities closed behind. Tarsal segments not lobed. A very large, cosmopolitan family: many species are incapable of flight and have their elytra fused together. They live amongst fungi or timber and in desert places. The larvae are cylindrical and very tough skinned, that of *Tenebrio molitor* being the well known meal-worm.

Fam. 77. **Trictenotomidae**. Antennae long with last three segments shortened and produced into angular processes. Strong and projecting mandibles. This family consists of but two genera of very large beetles found in Indian and Malayan forests.

Sub-order 5. PHYTOPHAGA

Tarsi really five-segmented, but only four segments are easily seen, the fourth being reduced to a small ring or tubercle at the base of the fifth. No beak or rostrum on the head.

Fam. 78. **Bruchidae.** Antennae serrated or pectinated. Elytra leave the posterior end of abdomen exposed. Posterior coxae enlarged. Prosternum short. A moderate-sized cosmopolitan family of small, plain beetles which lay their eggs chiefly in leguminous seed-cases e.g. pea-pods. The larva, as a rule, at first has legs, but loses these when it reaches the seed which it devours. *Bruchus pisi* and *B. fabae* do much harm to peas and beans.

Fam. 79. **Cerambycidae.** Antennae very long and their insertion embraced by the eyes, which become hollowed out anteriorly. Body elongate and straight. Pronotum narrower than elytra. The longicorns form a very varied, large, and widely distributed family of brightly ornamented and fair sized beetles. The larvae are soft white grubs with stout mandibles and often without legs; they burrow in the stems of trees and herbaceous plants. *Saperda populnea* in this way injures the Aspen in England.

Fam. 80. **Chrysomelidae.** Antennae short or moderate in length; their origin not as a rule indenting the eyes. An extremely large family of smallish convex, oval, brightly coloured, often metallic beetles which in both larval and imaginal state live on leaves. The larvae are usually fat grubs with three pairs of legs. *Haltica nemorum* is the turnip-flea, *Lema melanopa* eats corn leaves, *Crioceris asparagi* asparagus, and *Doryphora decemlineata* is the well known Colorado beetle which devours potatoes.

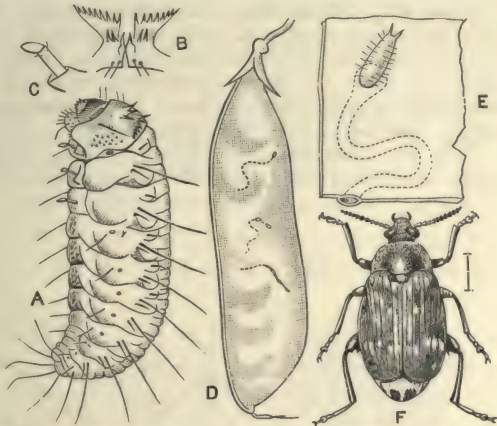


FIG. 468.—*Bruchus pisi* or pea-weevil. *A* young larva; *B* prothoracic spinous process; *C* post-embryonic leg, greatly magnified; *D* pea-pod, with tracks of entry; *E* portion of pod, with egg, and subsequently formed track, magnified; *F* imago (after Riley).

Sub-order 6. RHYNCHOPHORA.

Head produced into a snout or rostrum. Tarsi apparently four segmented, the third segment usually bilobed and covered with hair beneath. A very small additional joint is present at the base of the terminal joint, so that the tarsi are really five-jointed.

Fam. 81. **Anthribidae.** Labrum distinct. Antennae long and not elbowed, slightly clubbed. Rostrum short. Maxillary palps flexible. Third tarsal segment sunk in second. A moderate family of pretty beetles widely distributed but most abundant in warm climates. They probably eat decaying wood and fungi. *Platyrhinus latirostris* is British.

Fam. 82. **Brentidae.** Antennae straight, not elbowed. Rostrum straight and sometimes as broad as the head. Body elongated. A largish family of striking beetles found chiefly in the tropics, only two

species occurring as far north as southern Europe. The females bore in wood and bark by means of the sharp mandibles borne at the tip of the rostrum. There is often a marked sexual dimorphism in the members of this family. *Eupsalis*, *Cyphagogus*, etc.

Fam. 83. **Curculionidae.** Antennae usually elbowed. No labrum. Maxillary palps small and rigid and concealed within the mouth. The weevils form an enormous cosmopolitan family of over 20,000 very varied species. The larvae, which feed on plants and their products, are white, plump grubs devoid of legs. They cause much loss to the agriculturist. *Rhynchites* (Fig. 469), etc., etc.

Fam. 84. **Scolytidae.** Antennae clubbed and elbowed, maxillary palps short and rigid, but the rostrum extremely short and broad.

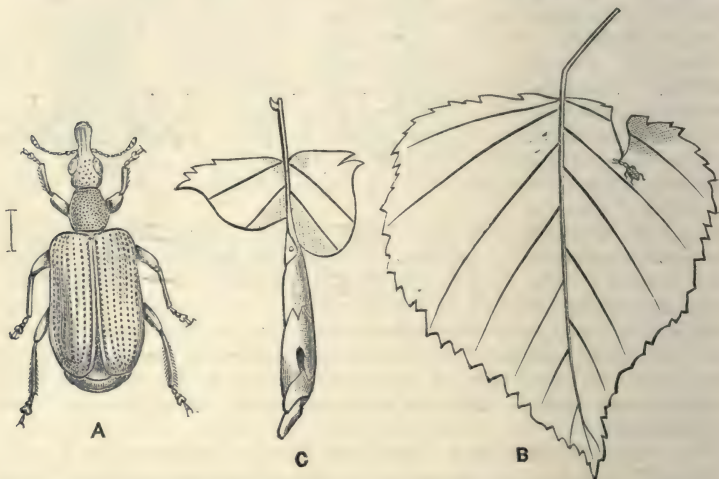


FIG. 469.—The leaf-rolling of *Rhynchites betulae*. Britain. A female beetle, magnified; B the beetle forming the first incision on a leaf; C the completed roll. (B and C after Debeij.)

The anterior tibiae are often toothed. A large family of small somewhat cylindrical beetles which with their larvae are usually found in galleries bored beneath the bark of trees. The pattern of the galleries varies with the species at work. The larvae are whitish, legless grubs. *Scolytus destructor* is the well-known "Elm beetle."

The following two families of Coleoptera do not fall within the limits of any of the larger groups and Sharp treats them as an appendix.

Fam. 85. **Aglycyderidae.** Three segments, the second lobed, to the tarsi. No rostrum. The family consists of a few species of the single genus *Aglycyderes* scattered over some of the islands of the globe.

Fam. 86. **Proterhinidae.** Tarsi with three easily visible segments, the second lobed; a minute additional joint present at the base of the terminal joint. The female has a rostrum, which hardly exists in the male. A single genus *Proterhinus*, found in the Hawaiian Islands, constitutes this family.

Order 20. STREPSIPTERA.*

Minute insects; males freely flying with large metathoracic wings, the mesothoracic pair being reduced to small dimensions (p. 615); no cross nervures. The parasitic female is reduced to a blind, almost formless sac.

These extraordinary insects are by some authorities classed with the Coleoptera. Their life history is as follows. The egg whilst still within the body of the mother, which it must be remembered is a parasite shut up inside the body of some Hymenopterous or Hemipterous host, gives rise to a small active, six-legged larva, known as a *triungulin*, so called from the three processes at the end of each tarsus.

A single mother may give rise to many hundreds of these microscopic, active larvae, which find their way on to the outside of the body of the host. Sooner or later they reach the larvae of the host, and boring their way through the skin enter these larvae and commence to feed on their fat body. When the host's larva pupates, the larval

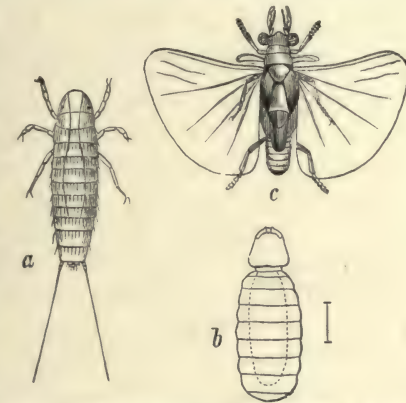


FIG. 470.—*Stylops childreni* (after Kirby). a larva
b female; c male.

parasite pushes one end of its body through the soft membrane uniting two of the abdominal segments. If this host-larva is about to turn into a male, the parasite in turn pupates, and from the pupa emerges the winged and active male Strepsipteron; but if the host-larva be destined to become a female, the parasite undergoes little but retrogressive change, until it becomes a female Strepsipteron so degenerate that it is still a matter of dispute as to which end represents the head and which the tail. The male seems to live but a very short time; in the case of *Xenos* about twenty minutes, whilst the male *Stylops* lives a day or two,

* Von Siebold, *Arch. Naturg.*, ix, 1843, p. 137. Newport, *Tr. Linn. Soc.* xx. 1851, p. 351. Nasonoff, *Zool. Centrbl.*, i, 1894. Meinert, *Ent. Meddel.*, v, 1896, p. 148, and *Ov. Danske. Selsk.*, 1896, p. 67. Brandt, *Hor. Soc. Ent. Ross.*, xiv, 1879.

the whole time being spent in a feverish search for mates. As a rule but one *Stylops*, or at most two or three, live in one host, but they are extraordinarily prolific. Ten specimens of *Xenos* have however been found in the body of the wasp *Polistes*. Some observers maintain that parthenogenesis is met with in this Order, but the matter requires renewed investigation.

Fam. 1. **Stylopidae.** With the characters of the Order. *Stylops*, *Xenos*.

Order 21. DIPTERA.*

Only one pair of wings, the mesothoracic, present; these are membranous; the hind-wings are represented by a pair of knobbed processes, the halteres; the thoracic segments are much fused; mouth parts piercing and sucking, variable. Metamor-

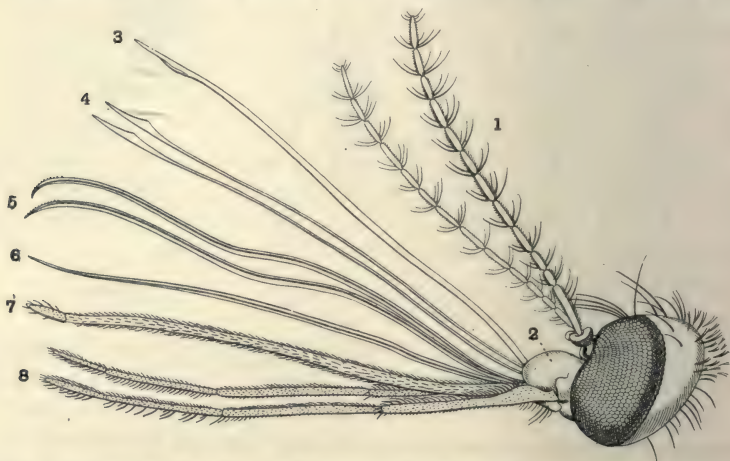


FIG. 471.—Mouth parts and head of *Anopheles maculipennis*, magnified (after Nuttall and Shipley). 1 antennae; 2 clypeus; 3 labrum and epipharynx; 4 mandible; 5 first maxilla; 6 hypopharynx; 7 labium; 8 maxillary palps.

phosis very complete. Larva usually a maggot, always without thoracic legs, and frequently with a minute, retractile head. Pupa either exposed with appendages more or less adherent to the body, or enclosed in a tough capsule and with appendages not adherent.

* Becher, *Wien. Ent. Zeit.*, i, 1882, p. 49. Brauer, *Verh. Ges. Wien*, xl, 1890, p. 273. Loew, *Smithson. Misc. Coll.* vi, 1862. Brauer, *Denk. Ak. Wien.*, xlii, 1880, p. 105. Williston, *Manual of North American Diptera*, 1896. Schiner, *Fauna Austriaca, Diptera*, 1860. Verrall, *British Flies*, London, in course of publication. F. V. Theobald, *Monograph of Culicidae*, Brit. Museum, 1907. Id., *Account of British Flies*, London, 1891–2, Pts. 1–5.

The Diptera form an enormous Order with over 40,000 described species. They are as a rule unpopular insects, seldom considered attractive in appearance and usually unpleasing in their habits, difficult to catch and in many cases to preserve. Probably the known species bear a smaller proportion to those that exist than is the case with the other Insect Orders.

Diptera are flies in the restricted sense of the word, and they are easily recognized by the possession of but one pair of functional wings, and frequently by the halteres * which replace the hinder pair (Figs. 365, 368). The latter, however, are not always readily observable.

The head (Fig. 471) is usually a somewhat flattened sphere, a large portion of whose surface is taken up by the faceted eyes, especially in the male. In about half the Diptera there is a curious concealed vesicle on the front of the head, called the *ptilinum*. During emergence from the pupa it is distended, and may help to rupture the enclosing shell of the pupa. In mature flies it is quite introverted, only a small space (*lunula*) under an arched suture indicating its existence. The antennae are usually short and exhibit variations useful in classification: usually they consist of but three segments; the two basal form the "scape," the terminal is called the "flagellum." It frequently bears a bristle called the "arista." The mouth-parts are complex and subject to great variation. In the gnat or mosquito we find the labium a soft, deeply grooved structure. In its hollow lie (i) a pair of wonderfully sharp and fine stylets, the mandibles; (ii) another pair of slightly coarser stylets, the first maxillae, which are provided with palps; (iii) a median style, the hypopharynx; and finally (iv) the labrum, with which is fused the epipharynx. The last named compound structure is so deeply grooved as to be almost a tube, and the fluid food of the insect passes up its hollow. The maxillary palps stand free of the proboscis. The labium ends in two diverging labellae which guide the piercing mandibles, maxillae, hypopharynx and labrum and epipharynx, as a player guides a billiard cue between his two fingers. Whilst these parts are being pressed (Fig. 472) into a yielding substance, the labium is bowed more and more

* ἀλτῆρες=dumb-bells which the Greek athletes used to give impetus in jumping.

backward. In the male the mandibles are absent and the hypopharynx has fused with the labium.

The head is joined to the thorax by an unusually flexible neck.

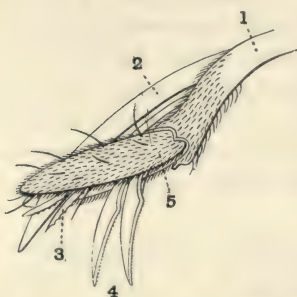


FIG. 472.—End of labium, labrum and epipharynx, mandibles and first maxilla of *Anopheles maculipennis*, magnified (after Nuttall and Shipley). 1 labium; 2 labrum and epipharynx; 3 first maxilla; 4 mandible; 5 labellae.

folding back of the wing, which in repose lies almost always flat and uncrumpled on the abdomen. The halteres are small knobbed structures which like the wings can vibrate rapidly. They are apparently sensory in function and in some cases possibly stridulating. The legs are slender, usually hairy. The tarsus has almost always five segments, and terminates in two well-developed claws, under each of which is a free pad, the pulvillus; a median empodium may also be present between the claws.

The abdomen may show as many as nine segments (Fig. 365) or as few as four. In the latter case a certain number of segments are withdrawn posteriorly into those in front and the first segment is concealed by the thorax. An ovipositor may be present.

In those Diptera which suck juices a powerful sucking pharynx, which expands under muscular effort, is found, also certain sacs

The segments of the thorax are much fused and their limits difficult to make out. The wings are membranous and, except in *Culicidae* (Fig. 473), devoid of scales; the "cells" are never numerous (Fig. 366). Very frequently at the posterior side of the base of the wing a notch separates a small lobe, the *alula*, from the rest of the wing; and still nearer the base one or even two more lobes may be seen called the *squama* (or *antitegula*) and *tegula*. These afford facilities for the



FIG. 473.—Scales on the edge of the wings of *Anopheles maculipennis*, magnified (after Nuttall and Shipley).

or reservoirs apparently belonging to the fore-gut, in which the juices are stored before digestion (Fig. 381). The usual number of malpighian tubules is four, but five occur in some families. Certain curious projections into the lumen of the rectum, termed anal papillae, are conspicuous in this order. These eminences are abundantly supplied with tracheae. There are a pair of prothoracic and a pair of metathoracic stigmata of complex design, and a varying number of pairs of abdominal stigmata much more simple in structure. The nervous system shows a great tendency to concentration, but in some families, e.g. the *Culicidae*, there are five or six abdominal ganglia.

Most Diptera are oviparous. The larva which leaves the egg is usually an eruciform maggot (Fig. 474, etc.), without true legs. "Pseudopods" and other aids to locomotion may exist. The head is usually small and in the true maggots may be much reduced, practically invisible, and tucked into the body. The larvae may be peripneustic, i.e. with stigmata arranged along the sides of the body; or amphipneustic, with only two pairs of stigmata, one at the posterior end of the body, the other near the anterior end; or metapneustic, that is, with only one pair of stigmata, at the posterior end. Many dipterous larvae are aquatic, and then they are often metapneustic, and penetrate the surface film with the part of the body bearing the stigmata, thereby exposing the latter to the air. Others are found in carrion, amongst plants, and in decaying organic matter generally, while many dipterous larvae are parasitic in the bodies of other insects. Either the last larval skin is cast away, and the pupa is an obtected pupa, lying exposed, but protected by a hardened chitinous exudation, which may fasten the appendages more or less to the body; or the creature changes to a delicate pupa with free appendages, within the last larval skin, which remains as a tough enclosing shell, frequently called the *puparium*. This latter pupa is spoken of as a coarctate pupa (p. 651). During the pupa-stage there is a considerable amount of histolysis, the tissues breaking down and reconstituting themselves usually from certain centres of growth termed *imaginal discs* (p. 651). In some forms such as *Chironomus* and the *Culicidae* many organs of the imago are already formed in the last larval stage.

For purposes of identification the Diptera may be divided into five groups: (i) *Nemocera*, (ii) *Brachycera*, (iii) *Aschiza*, (iv)

Schizophora and (v) Pupipara. The first two groups have an obteeted pupa and the imago emerges through a dorsal slit in the pupa-case. In the case of the Aschiza and Schizophora the pupa-case is formed of the skin of the last larval stage, though this is altered by chitinous deposits and shrinkage, and the imago emerges by a splitting at the anterior end. The last group, Pupipara, consists of certain aberrant flies and is probably not a natural assemblage.

Group 1. NEMOCERA.

Antennae slender, at least seven segmented, not ending in a bristle. Palps with four or five segments. They are long, as are usually the legs and body.

Fam. 1. Cecidomyiidae. Minute delicate flies with very few wing nervures. The Gall-midges form a very extensive and cosmopolitan family. Antennae elongated with rings of hairs. Ocelli very rarely present.

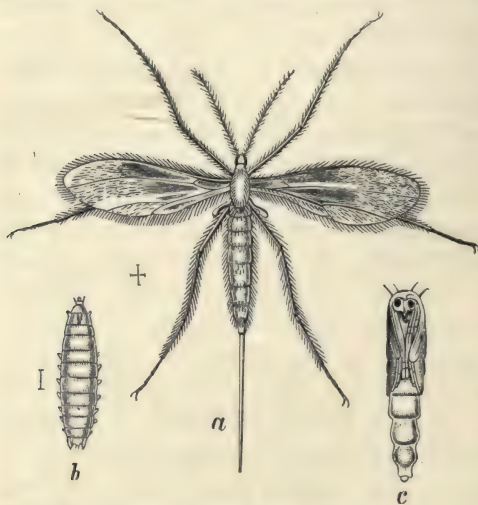


FIG. 474.—*Cecidomyia tritici* (after Wagner). *a* female with protruded ovipositor; *b* larva; *c* pupa.

The head is large, the antennae are monili-form with thirteen segments in the female and twenty-four at least in the male. There are eight segments in the cylindrical abdomen. The larvae are small maggots with as many as thirteen postcephalic segments. The ventral surface of the first of these segments bears a chitinous process of debatable function. Many of the larvae burrow in plants and their presence produces galls and other vegetable malformations. *Cecidomyia destructor*, the

Hessian fly, weakens the stems of Wheat and causes them to bend over, *C. tritici* attacks the flowers of the same plants. Paedogenesis occurs in *Miastor* and in *Oligarces*, the larvae producing young which live on the tissues of their parent and finally leave its body by boring a hole in its skin.

Fam. 2. Mycetophilidae. More robust than the previous family with more wing nervures and with ocelli. Antennae without whorls of hairs. Legs spiny. This cosmopolitan family includes the flies known as Fungus midges or Fungus-gnats as the larvae live amongst fungi and decaying plants. They are long, fleshy maggots, some of which spin a cocoon before pupating, or make an earthen cell. Many, e.g. *Sciara*, secrete a mucus,

and as they are gregarious and their respective mucous sheaths fuse together, whole colonies in bands or ropes several yards long may be seen migrating. *Mycetobia* British, has terminal stigmata.*

Fam. 3. **Blepharoceridae.** No discal cell on the iridescent wings. Eyes divided into an upper half with large ommatidia and a lower half with small. This family is European and American. The flies hover with a dancing flight in the air. The larvae are very remarkable, and more like minute Polychaets than maggots. They cling to submerged stones by means of a row of ventral suckers. The pupa is also aquatic. *Liponeura* is European, *Blepharocera* is common in the cooler parts of N. America.

Fam. 4. **Culicidae.** Antennae with rings of hairs forming a dense plume in the male. Mouth-parts conspicuous and forming a piercing proboscis (Figs. 376, 471, 472). Complex nervuration (Fig. 366). This extensive and widely distributed family comprises the gnats and mosquitoes, neither of which terms has any precise zoological significance. A mosquito may perhaps be defined as a gnat that sucks blood, but it must be remembered that it is only the female that "bites." The normal food of the *Culicidae* is plant- or fruit-sap, and it has been suggested that a meal of blood is necessary before eggs can be laid. This however can hardly be the case, as in the waste lands of the north there must be countless millions of gnats which never get an oppor-

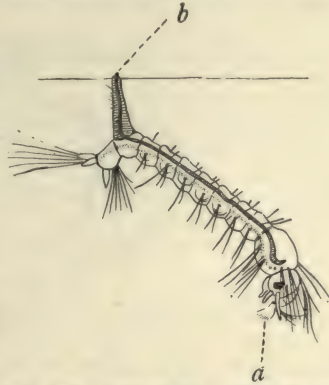


FIG. 475.—Larva of *Culex pipiens* hanging on to the surface-film by its drawn-out respiratory tube, magnified. *a* bunch of hairs on the head which sweep food particles into the mouth; *b* respiratory tube.

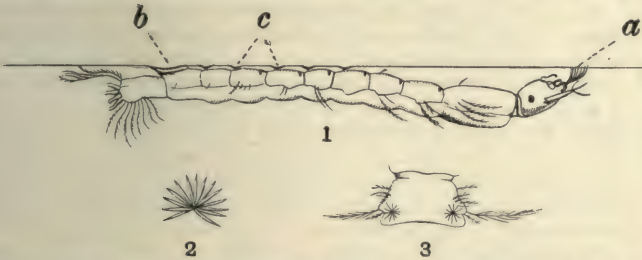


FIG. 476.—Larva of *Anopheles maculipennis* hanging on to surface-film. *a* brush of hairs on the head (which is reversed so that the ventral side is uppermost) which brush food-particles into the mouth; *b* respiratory plate; *c* hairs which cling to the surface film. 3 dorsal view of an abdominal segment showing the lateral hairs and the dorsal whorl of hairs; 2 a dorsal whorl very highly magnified (after Imms).

tunity to taste blood. The eggs are usually dropped on the surface of the water or on aquatic plants. The larvae breathe by a pair of stigmata situated posteriorly. In the genus *Culex* these open at the end of a

* A very remarkable scale-bearing Mycetophilid larva is described by Nils Holmgren, *Zeitschr. Wiss. Zool.*, lxxxviii, 1907, p. 1.

protuberance which diverges dorsally from the penultimate segment, and so gives a Y-shaped appearance to the larva, whose body hangs down into the water (Fig. 475). The larva of *Anopheles* lies flat beneath the surface-

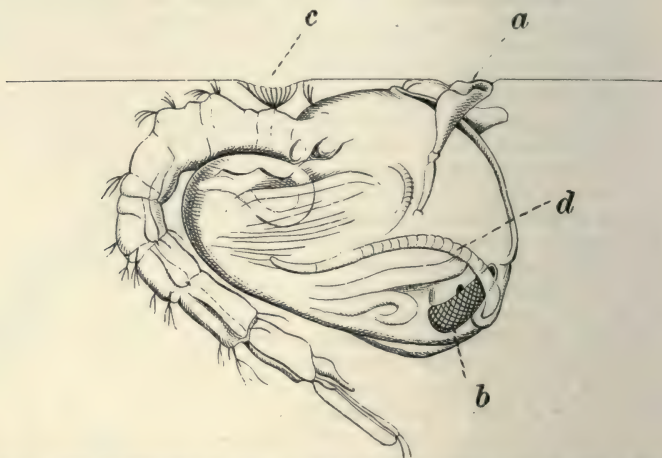


FIG. 477.—Pupa of *Anopheles maculipennis* attached to the surface-film of water, magnified (after Nuttall and Shipley). *a* breathing trumpet; *b* eye; *c* palmate hairs on the anterior end of the abdomen which clings to the surface-film; *d* antennae.

film, attached to it by paired palmate hairs and by the saucer-like opening of the two stigmata (Fig. 476). The pupae also hang on to the surface-film and breathe through two trumpet-like stigmata situated behind the head (Fig. 477). The larva of *Corethra* has no stigmata. The imagos are peculiar amongst Diptera in the possession of scales both on the body and on the wings. Gnats often occur in quite incredible numbers, dancing in the air in dense clouds. The imagos frequently live through the winter hidden away in obscure outhouses and corners: the eggs and also the larvae survive the cold of winter. Lately this family has attracted much attention, as it has been shown that *Anopheles maculipennis*, a widely distributed species, common in Britain, is the distributing agent (with other species) of the Haematozoon which causes malaria; and is also, together with *Culex*, the distributor of certain Filarias which cause various disorders in tropical countries (vol. 1, p. 289); whilst *Stegomyia fasciata*, a common gnat, plays a similar rôle in the case of Yellow-fever.* Other genera are *Aedes*, *Megarhinus*, and *Psorophora*.

Fam. 5. **Chironomidae**. Small flies with narrow wings, and no projecting rostrum. Long antennae, plume-like in male, and long legs. No ocelli. This family includes forms popularly termed gnats and midges. It comprises a large number of species and is universally distributed. Like the Culicidae the species frequently form dense, dancing swarms. Their larvae are aquatic, without stigmata; and often blood-red from the presence of haemoglobin; hence their name of blood-worms. They often form tubes of mud or sand. A few are marine. *Chironomus* is said to have some two hundred British species. *Ceratopogon* is the midge which causes much

* The disease-conveying gnats play so large a part in human economy

annoyance in Scotland, where its presence in conjunction with that of the kilt is said to have given rise to the Highland Fling.

Fam. 6. **Orphnephilidae.** Small, hairless flies, brown or yellow in colour, with very large eyes and a two segmented antenna bearing a bristle, the second segment and the bristle are however compound. Little is known of the members of this family. The only genus *Orphnephila* occurs in Europe, Britain, and North America.

Fam. 7. **Psychodidae.** Minute, fragile, hairy, moth-like flies with broad wings covered, as are the antennae, with hair. No ocelli. These feeble little flies are found on window-panes and under leaves. They are widely distributed. The larvae have both tracheal gills and stigmata, and are amphibious. *Pericoma* is British. *Phlebotomus* sucks blood.

Fam. 8. **Dixidae.** Small, gnat-like flies which do not bite. The larva has two leg-like projections on the first and second abdominal segments. This family consists of but one cosmopolitan genus, *Dixa*, with four British species. They frequent moist forest glades and the larva and pupa are aquatic.

Fam. 9. **Tipulidae.** Very large, slender flies with long legs. Wing nervures numerous, often branching (Fig. 367). A V-shaped suture on the thorax. The cylindrical abdomen of seven or eight segments ends in a pair of claspers in the male, and in an ovipositor in the female. A numerous and widespread family whose members are known as Daddy-long-legs or Crane-flies. The head is conspicuous, with a slender, rather long neck, and no ocelli. The larvae are either aquatic, or are tough grubs living underground and doing much damage by eating the roots of crops. They are termed Leather-jackets. Some of the aquatic larvae (e.g. *Bittacomorpha*) have the two posterior segments of the body drawn out into a very long slender tail, no doubt respiratory in function. The pupae project from the ground when ready to emit the adult form; they are in many ways like those of Lepidoptera, but have a pair of respiratory horns or tubes on the thorax. The imagoes are commonest in the late summer in woods

that we subjoin a table of the incriminated species, indicating, by the figure in front of each, the disease it is instrumental in spreading.

Sub-fam. <i>Anophelinae.</i>		1, 4. <i>Pyretophorus costalis</i> Loew.
1, 5. <i>Anopheles bifurcatus</i> Linné.	1, 5. „ <i>superpictus</i> Grassi.	
1, 5. „ <i>maculipennis</i> Meig.	„ <i>chaudoyei</i> Theob.	
1. „ <i>martini</i> Laveran	4. <i>Nyssorhynchus albimanus</i>	Wied.
1. „ <i>pursati</i> Laveran		
1. „ <i>vincenti</i> Laveran		
1. „ <i>formosensis</i> Tsuz.		
1. „ <i>algeriensis</i> Theob.		
1. <i>Myzomyia lutzii</i> Theob.		
1. „ <i>culicifacies</i> Giles.		
1. „ <i>listoni</i> List.		
1, 4. „ <i>funesta</i> Giles.		
1. „ <i>hispaniola</i> Theob.		
4. „ <i>rossii</i> Giles.		
1. <i>Myzorhynchus paludis</i> Theob.		
1. „ <i>coustani</i> Laveran		
1. „ <i>jesoensis</i> Tsuz.		
4. „ <i>nigerrimus</i> Giles.		
1. „ <i>sinensis</i> Wied.		
1, 5. „ <i>pseudopictus</i> Grassi.		

1 = *Malaria* (human). 2 = *Malaria* (avine). 3 = *Yellow-Fever*. 4 = *Filariasis* (human). 5 = *Filariasis* (canine).

and pastures, where they sometimes swarm. The number of species is very great. *Tipula*, *Phalacrocer*a, *Cylindrotoma* are amongst the British genera.

Fam. 10. **Bibionidae**. Fairly large flies, weak on the wing. Antennae short and stout. The male has very large eyes, and there are three ocelli. The larvae are almost caterpillar-like, with a distinct, chitinous head and sometimes with a number of spines on the body. They live frequently on decaying vegetable matter. *Bibio* often occurs in large numbers in England in the early spring and summer. *Scatopse* is said to breed in drains, etc. In some species there is a marked sexual difference, the females being red or yellow, the males black.

Fam. 11. **Simuliidae**. Small flies with a "humped" thorax. Broad wings, short legs, antennae with no hairs. No ocelli. These flies, all included in the one cosmopolitan genus *Simulium*, are known as sand-midges or buffalo-flies. The eyes are enormous in the males. The females, which often occur in large swarms, eagerly suck blood, and so voracious are they that poultry, cattle and even man have been known to succumb to their combined attacks. The larvae are aquatic and live in running water: they spin pupa-cases under water from which the imagos emerge and float to the surface, each surrounded by a bubble of air.

Fam. 12. **Rhyphidae**. A discal cell present in the wings, which are broad and rounded. The species of this family of two or three widely distributed genera resemble miniature Tipulids. The larvae live in decaying plants, cow-dung and foul water. *Rhyphus fenestralis* frequents window-panes.

Group 2. BRACHYCERA.

Antennae variable, usually with three distinct segments, rarely with more than seven: either an arista is present, or the flagellum terminates in a slender, indistinctly segmented, appendage. Palpi one- or two-jointed. Larvae usually, maggots with retracted head.

Fam. 13. **Stratiomyidae**. Stout flies with three-segmented antennae with a terminal portion of obscure segments frequently bearing an arista. Tibiae not spined. Wings smallish with nervures better developed anteriorly than posteriorly. A large, varied and rather ill-defined family of about one thousand described species, some fifty of which are British. The body is often marked with yellow and green or metallic tints, and is not hairy. The larvae are aquatic or live in damp earth or moss. The pupa is formed inside the last larval skin, and floats in water or is subterranean. *Stratiomys* is sometimes called the soldier-fly.

Fam. 14. **Leptidae**. The Snipe-flies are slender with spotted or velvety bodies. Antennae with three joints ending in a bristle. Large wings. They move slowly and are easily caught. They prey on small insects, and the larvae which are often subterranean are also predaceous. The pupae are protected by earthen cells. *Atherix*.

Fam. 15. **Xylophagidae**. Antennae longer than in *Leptidae* and with a complex third joint. These flies are slender and live on the sap of plants. Their larvae live under bark and suck the juices of other insects. *Rhachicerus*.

Fam. 16. **Coenomyiidae**. Thick, heavy flies. Larvae living in burrows in the earth, generally near decayed logs. Only one genus *Coenomyia*, which is found on both sides of the Atlantic.

Fam. 17. **Tabanidae.** This family includes the Horse-flies or Gad-flies sometimes termed Cleggs or Breeze-flies. They are stout, large flies, with a fleshy proboscis bearing stylets capable in the female of piercing the skin. Antennae projecting, with four segments. Eyes very large especially in the male. Well developed squama. These are dangerous flies usually found near inland water. The females suck the blood of horses, cattle and man, and are said to transmit the bacillus of anthrax from one animal to another. Members of the common British *Tabanus* attain a length of one inch, and are conspicuous by their loud humming. The larvae are maggot-like, live in damp earth and eat snails and insect grubs. Some 1,500 species are known. *Pangonia*.

Fam. 18. **Acanthomeridae.** Antennae end in a seven-segmented process with a terminal style. Squama rudimentary. Proboscis short. *Acanthomera* and *Rhaphiorhynchus* are the two American genera which compose this family. Some specimens attain a length of two inches and are the largest flies known.

Fam. 19. **Therevidae.** Smallish, slender flies with a weak fleshy proboscis. Short three-segmented antennae, pointed. Very slender legs. The larvae, with nineteen segments, frequent decaying wood; the imago is said to prey on other insects. *Thereva*.

Fam. 20. **Scenopinidae.** Small, black, active flies, with three-jointed antennae. Proboscis not projecting. No empodium. A very small family of flies mostly found on windows. The elongated white larvae frequent carpets and woollen fabrics and decayed wood, and are said to live on the larva of the "carpet-moth."

Fam. 21. **Nemestrinidae.** Medium sized, stout flies with in some species a very long proboscis. Short antennae of three joints with a jointed terminal appendage. Wing nervures very complex for a fly. The long proboscis sucks nectar from flowers. The larva of *Hirmoneura* is parasitic on that of a Lamellicorn beetle (*Rhizotrogus*) which feeds on turf, although the egg is laid in the burrows of some wood borer, from which the larva emerges and migrates by the aid of the wind.

Fam. 22. **Bombyliidae.** Bee-like flies of stout build, hairy. The three-jointed antennae end as a pointed process. Proboscis often long. Mandibles and first maxillae piercing. Weak legs and many-celled wings. *Bombylius* poises in the air almost motionless and then darts away with almost invisible rapidity. It haunts the sunny spots of woods and glades and sucks the nectar of flowers. The larvae of some Bombyliidae make their way into the nests of certain Mason-bees and, after gently absorbing the juices of the pupae of their hosts, pupate. The pupa is capable of breaking down the masonry of its prison. The larvae of other species render a public service by feeding on the eggs of locusts. The family is large and widely distributed.

Fam. 23. **Acroceridae.** Flies of medium size, with small head bent



FIG. 478. — *Pangonia longirostris*. $\times 1$. Nepal (after Hardwicke).

down under the strongly convex, humpbacked thorax. Wings small, but the squama hides the halteres. The flies are often metallic and brightly coloured. This is a small group with few species, but two genera, represented by *Ogcodes gibbosus* and *Acrocera globulus*, are British. The larvae are parasitic in spiders or in their egg-sacs.

Fam. 24. **Lonchopteridae.** Slender, minute flies with lance-like wings with feeble nervuration. A small family of very isolated structural characters. The larvae live on the earth under leaves, etc. *Lonchoptera*, the only genus, is widely distributed.

Fam. 25. **Mydidae.** Large flies, with yellow and red bands and knobbed antennae. Wings with complex nervures, often pigmented. This family is chiefly tropical but reaches Southern Europe, and the American *Mydas* spreads into the S. United States. The flies are predatory, and the larvae live in decaying trees and probably prey on wood-boring insects.

Fam. 26. **Asilidae.** Large, strong, hairy flies. The proboscis forms a short, stout, murderous beak. The thorax is narrowed in front and the head appears broad. Feet well developed with large claws, pulvilli and bristle-like empodia. The Robber- or Hawk-flies form an enormous family with some 3,000 species. They are amongst the most rapacious of insects, attacking equally wasps, bees, tiger-beetles, dragon-flies, etc. Some of them closely resemble the Hymenoptera on which they prey. The larvae live in the earth or in wood, and feed on Coleopterous larvae and eggs of grass-hoppers, etc. *Asilus*. *Laphria* resembles a *Vespa*.

Fam. 27. **Apioceridae.** Medium-sized black and white flies with transparent wings. No empodium. A small family of two genera confined to the eastern side of the Pacific and to Australia. They are allied to the Asilidae. *Apiocera*.

Fam. 28. **Empididae.** Smallish, slender, dingy flies, with little or no hair except on the long legs. Predaceous, attacking and devouring other flies. Proboscis long and slender. The ovipositors of the female and the claspers of the male are often conspicuous. This is a family of some eleven hundred species, nearly two hundred of which are British. They frequent woods and dance vigorously up and down in the air, and some of them carry little webs of silk. The cylindrical larvae live under leaves or in other decaying vegetation.

Fam. 29. **Dolichopidae.** Slender, moderately sized or small flies with blue or green or golden metallic sheen. Legs long. Proboscis short and fleshy. A family of about the same size and with almost as many British representatives as the preceding. The males are curiously and diversely ornamented. The larvae live under bark, or amongst decaying plants. The pupa is protected by a cocoon.

Group 3. ASCHIZA.

Antennae of not more than three segments, bearing an arista or bristle which may be feathered, and is very rarely terminal. No frontal arched suture over the base of the antennae.

Fam. 30. **Phoridae.** Small flies with two very conspicuous dark veins near the front edge of the wings, very convex thorax and two-jointed antennae with a bristle. A small and isolated, but widely distributed, family whose members haunt window panes. The larvae live on a variety of decaying plants and attack also such animals as snails and chrysalids. The pupa case is the last larval skin, hardened. *Trineura*.

Fam. 31. **Platypezidae**. Small flies, with three-segmented antennae and a terminal bristle; the first two segments are short, the last is longer. The tarsi of the hind legs are very broad. No empodium. A small family of little, blackish flies which frequent shady places. The larvae have a flattened shape and their edges bear bristles. They live between the "gills" of mushrooms and toad-stools. *Opetia*, *Platycnema*, *Platypeza* and *Callomyia* are the four genera with British species.

Fam. 32. **Pipunculidae**. Small flies with very short antennae with a non-terminal bristle. The head is very large, nearly spherical, and composed almost entirely of the enormous, almost contiguous, eyes. A small family with three British genera and perhaps twelve species. The larvae live parasitically within the bodies of Homopterous Hemiptera. When about to undergo transformation, they emerge from their hosts. and pupate within the last larval skin, usually in the ground, occasionally exposed on leaves. *Pipunculus*.

Fam. 33. **Conopidae**. Abdomen pedunculated like a wasp's and often yellow-banded. The head is large and swollen. Few or no bristles on the dorsal surface. Not a very large family, some members of which, e.g. *Conops*, pass their larval life inside the abdomen of Bumble-bees, Wasps, etc.

Fam. 34. **Syrphidae**. Stoutish flies with fleshy, retractile proboscis, recognizable by the presence of an extra longitudinal nervure, the "vena spuria," between the third and fourth. Head and eyes large. The family is large and cosmopolitan. The Hover-flies vary much in colour and many of them resemble Hymenoptera; they frequent flowers and may often be seen hovering in the sunlight. The habits of the larvae vary. Those of *Syrphus* devour plant lice. *Volucella* larvae live in bee- and wasp-nests, eating the grubs of their host. Others feed on decaying vegetable matter or wood. The rat-tailed maggot of *Eristalis* lives in foul water, or possibly even in carcases. The curious mollusc-like larvae of *Microdon* lives in ants' nests.

Group 4. SCHIZOPHORA.

Three joints to the antennae and an arista, or bristle not borne terminally. An arched frontal suture overlies the base of the antennae as a rule.

This group includes both a large number of families of very small flies which are but little known, and also the most typical of all flies e.g. the *Muscidae*. The former collection, known as the *Muscidae acalyptrate*, are divided into a number of families of varying valency, and they eminently require revision. They are called "acalyptrate" because the squama is either absent, or when present does not cover the halter. They will be barely mentioned here.

Fam. 35. **Doryceridae**. The larva of *Dorycera* burrows in the leaves of aquatic plants.

Fam. 36. **Tetanoceridae**. The larvae are said to have but eight segments.

Fam. 37. **Sciomyzidae**. Brown or greyish unattractive flies which haunt high grasses and bushes.

Fam. 38. **Celyphidae**. In *Celyphus* the enlarged highly polished scutellum overhangs and hides the abdomen, which is much reduced, and also the wings.

Fam. 39. **Sepsidae**. Small, polished, flies breeding in dung or

decaying matter (*Sepsis*) or in cheese and fat (*Piophilæ*). The cheese skipper is the larva of *P. casei*. They also injure dried and smoked meat.

Fam. 40. **Chloropidae (Oscinidae)**. The larvae live in the stems of wheat and grass and do much damage, or mine in the leaves of such plants as the beet-root; others act as scavengers. In the autumn the imagoes sometimes turn up in countless swarms, usually in the same building at intervals of some years. They are amongst the commonest insects to get into eyes whether of man or beasts. The Frit-fly, *Oscinis frit*, and the Gout-fly, *Chlorops taeniopus*, are well known corn pests.

Fam. 41. **Ulidiidae**.

Fam. 42. **Platystomidae**.

Fam. 43. **Ephydriidae**. Some of this family breeds in salt lakes such as those of Utah, and a few occur in urinals. They exist in vast numbers in many of the Mexican lakes, where both the larvae and flies drift in heaps on to the shores and are collected by the Indians and made into palatable cakes.

Fam. 44. **Helomyzidae**. Dark, small flies frequenting the shade and twilight, laying their eggs in animal dejecta or amongst fungi.

Fam. 45. **Dryomyzidae**.

Fam. 46. **Borboridae**. Small, dark flies with clear wings. Some species of *Borborus*, which is a British genus, are however wingless. They breed in dung and have some use as scavengers.

Fam. 47. **Phycodromidae**. Small greyish flies with a darker abdomen. They occur on the beaches of both seas and lakes and seem to breed amongst the vegetable jetsam.

Fam. 48. **Thyreophoridae**.

Fam. 49. **Scatophagidae (Scatomyzidae)**. Moderate-sized, slender flies, frequently hairy. They breed in the dung of various animals and are generally known as dung-flies.

Fam. 50. **Geomyzidae**. A small family of small flies whose larvae, in the cases known, mine in the leaves of grass and corn.

Fam. 51. **Drosophilidae**. Small flies which haunt decaying fruit, etc., in which their larvae live. They also occur in tinned fruits and in pickles and amongst the refuse of cider- and wine-presses. *Drosophila*.

Fam. 52. **Psilidae**. These generally dark flies are met with on the leaves of bushes and undergrowth. The larvae, when known, burrow in plant-stems or in fleshy roots. *Psila rosae* causes the disease of "rust" in carrots.

Fam. 53. **Micropezidae (Tanypezidae)**. Moderate-sized, slender flies with long legs which frequent decaying matter both animal and vegetable. Their larvae are unknown.

Fam. 54. **Trypetidae**, Fruit-flies. Spotted yellow or brown flies with mottled wings. The larvae live in galls on the stems or fruits of plants. In America *Trypeta pomonella* does much harm to apples, as does *Ceratitis capitata* to peaches.

Fam. 55. **Sapromyzidae**. Wings rarely spotted. The larvae sometimes live under bark or in the tunnels bored in wood by other insects or in rotten vegetation.

Fam. 56. **Lonchaeidae**. This family is often included in the preceding. Its larvae have been found in stems and roots and in dung. *Lonchaea*.

Fam. 57. **Rhopalomeridae**.

Fam. 58. **Ortaliidae**. Usually metallic flies with spotted or striped wings. The larvae occur under the bark of certain trees and in fruit, but

it is thought that they only enter the burrows of other insects and do not mine themselves. *Camptoneura*.

Fam. 59. **Agromyzidae**. Small flies whose larvae burrow in plants largely in the leaves, or devour Aphides. *Leucopsis*.

Fam. 60. **Milichiidae**.

Fam. 61. **Oethophilidae**.

Fam. 62. **Heteroneuridae**. Slender, yellow or dark flies whose larvae live in damp, dirty spots or under bark.

Fam. 63. **Cordyluridae**.

Fam. 64. **Diopsidae**. The head is broadened and sometimes produced into very elongate lateral projections, which bear the eyes. These flies frequent shady woods. They are not found in Europe.

This family is the last of the *Muscidae Acalyptatae*. The six following families may be grouped together as *Muscidae Calyptatae*: in them the squama forms a calypteron covering the halter.

Fam. 65. **Anthomyiidae**. Resemble house-flies, but the ulnar nervure (4th longitudinal) is straight. Bristle of antenna naked or feathered. Four or five abdominal segments visible. A large, cosmopolitan, unattractive and generalized family with affinities to the *Muscidae acalyptatae*, the *Tachinidae*, the *Muscidae* and the *Sarcophagidae*. The larvae are flattened maggots with posterior stigmata, and of very varying habits. *Anthomyia brassicae* is destructive to cabbages, and on the other hand *A. cana* and *A. angustifrons* destroy locusts.

Fam. 66. **Tachinidae**. Bristle on antenna bare or nearly so. Abdomen with four to six bristly segments visible. First posterior cell almost or completely closed. A large, and to man beneficial family of flies, since their larvae live in and destroy other insects, especially caterpillars, many of which are injurious to crops. The larva devours the interior of its host, but at first at least does not eat the more essential organs, so that the host lingers on until the larva is fully grown, the parasite then leaves the body of the caterpillar and pupates on the ground. *Miltogramma* (British) may lay its egg in flies of the family *Tabanidae* which have been previously captured by the Hymenopteran *Bembex* as food for its own young. *Thrixion* is parasitic on Orthoptera. Some two hundred species of this family are British.

Fam. 67. **Dexiidae**. This family resembles the last mentioned, but the bristle on the antenna is pubescent, the legs are longer and some species are brilliantly coloured. The larvae are parasitic in insects and snails. *Dexia*, *Rutilia*.

Fam. 68. **Sarcophagidae**. The bristle of the antennae is feathered proximally and hair-like distally. Some species are viviparous and *Sarcophaga magnifica* causes much trouble by laying its maggots in sores.

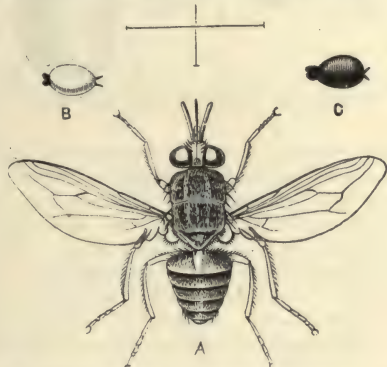


FIG. 479.—The Tsetse fly (*Glossina morsitans*). A the fly with three divisions of the proboscis projecting; B adult larva; C pupa. (From Sharp.)

Most species have larvae parasitic in other insects. *S. carnaria* is a common British form which resembles the Blow-fly.

Fam. 69. **Muscidae.** Antennal bristle feathered. This family includes the house-fly, blue-bottle, etc. They lay their eggs in dead flesh or dung. The common house-fly—*Musca domestica*—usually deposits its eggs in stable manure, the larvae live on their surroundings for less than a week and then pupate, and the imago emerges about a fortnight after oviposition (Hewitt, *Q.J.M.S.*, 51, 1907, p. 395). Two common species of blow-fly are found in Britain, *Calliphora vomitoria* and *C. erythrocephala*. *Glossina* includes the dreaded Tsetse-flies of Africa (Fig. 479).

Fam. 70. **Oestridae.** Large, hairy flies with very short antennae bearing a segmented bristle.

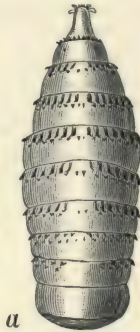


FIG. 480.—*Gastrophilus equi* (after F. Brauer).
a larva; b male.

Posterior part of wing with few nervures. Mouth parts often aborted. The larvae of the Bot-flies live in Vertebrates and for the most part in Mammals. The family is a small one, but there are some ten British species, which attack cattle and deer. *Gastrophilus equi* lays its eggs on the hair of horses. On hatching they set up an irritation which causes the horse to lick the place, and the larvae being thus swallowed, come to rest in the stomach, to the walls of which they attach themselves until

ready to pupate, when they pass out with the excreta. *Hypoderma lineata* and *bovis* lay eggs on the legs of cattle. Later, the larvae are found causing the "warbles" or tumours under the skin of the back. They are probably licked off the legs and swallowed, and burrowing through the gut-walls, reach their position under the skin, but, at present, there is some doubt as to the route by which they reach their final destination. When full-grown they emerge from the warbles, fall to the ground, and pupate therein. *Oestrus ovīs* places its larvae—it is viviparous—in the nostrils of sheep, whence they wander into adjacent cavities.

Group 5. PUPIPARA.

A group degraded by parasitism. The members for the most part suck blood. They are viviparous, producing larvae which immediately pupate.

Fam. 71. **Hippoboscidae.** Wings large, small or absent. The body and legs are flattened. The singly-segmented antennae are hidden and



FIG. 481.—*Hippobosca equina*.



FIG. 482.—*Melophagus ovinus*.

the mouth-parts are much modified. *Hippobosca equina* (Fig. 481) is the Horse-or Forest-fly well known in Britain. *Melophagus ovinus* (Fig. 482), the sheep tick, has lost all resemblance to normal Diptera; it is wingless and creeps amongst the hairs of sheep. There are other species which attack birds, and these for the most part retain their wings.

Fam. 72. **Braulidae.** Antennae not so well hidden as in the preceding family, from which this one differs also in the structure of the mouth-parts. Eyes imperfect. This family consists of a single, minute, wingless species, *Braula coeca*, which lives on bees, usually on the thorax (Fig. 483).

Fam. 73. **Streblidae.** Winged insects with halteres, and narrow, free head. The insects of this family are rare and live on bats. The larvae are said to live in the dejecta of their hosts.

Fam. 74. **Nycteribiidae.** Head upright or bent back on to dorsal surface of thorax. Wings absent. Legs long, borne on the upper surface of a chitinous plate formed by the meso- and meta-sterna; so that the



FIG. 483.—*Braula coeca*. $\times \frac{1}{2}$. (after Meinert).

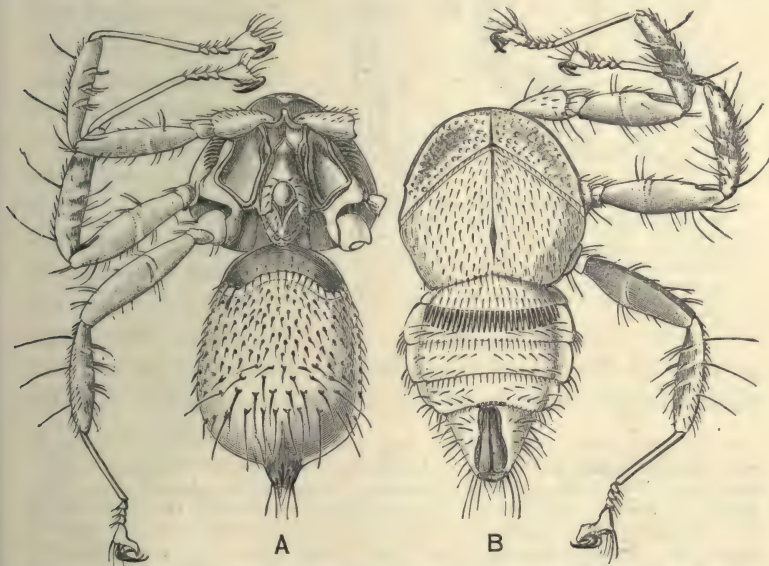


FIG. 484.—*Nycteribia*, sp., from *Xantharpyia straminea*. Aden. A upper surface of female with head in the position of repose; B under surface of male. $\times \frac{1}{2}$. From Sharp.

upper surface may appear at first sight to be the under. These peculiar Insects are, like the Streblidae, parasites on bats. *Nycteribia*.

Order 22. HYMENOPTERA.*

Four membranous wings with few nervures; the anterior abdominal segment fused or partly fused with the thorax, the "waist" when present being behind this; the females have an ovipositor which may or may not be retractile; mandibles well developed. Metamorphosis complete: the pupa has its appendages free.

The Hymenoptera include Bees, Wasps, Ants, Sawflies, Gall-flies, Ichneumon-flies, etc., and in this order the Insects, and indeed the Invertebrata as a whole, attain their highest social and psychical standard.

The head is free and very mobile. By a kind of dislocation the pronotum remains fused with the rest of the thorax, whilst the other

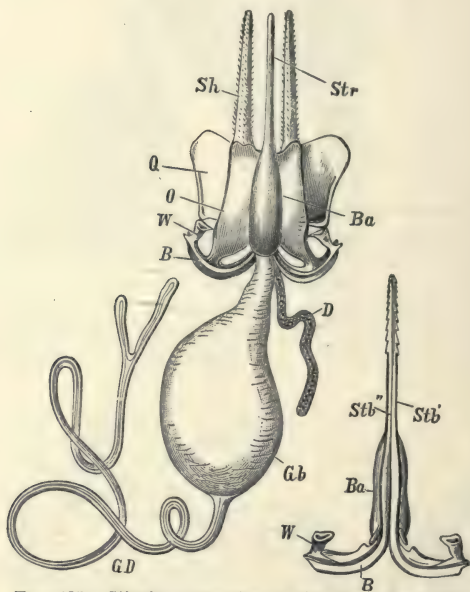


FIG. 485.—Stinging apparatus of the honey bee from the dorsal side (after Kraepelin). *GD* poison gland; *Gb* poison reservoir; *D* gland; *Str* grooved piece (director); *Ba* swollen base of the grooved piece; *B* curved root of the same; *W* angular piece; *Sh* sheath of spine; *O* oblong plate; *Q* quadratic plate; *Stb'*, *Stb''* the two piercing spines on the ventral side of the grooved piece.

sclerites of the prothorax with the first pair of legs are thrown a little forward and act largely in conjunction with the

* Cameron, *Brit. Phyt. Hym.*, Ray Soc., 1882–93. Fabre, *Souvenirs entomologiques*, 3rd sér., 1886. Lubbock, *Ants, Bees, Wasps*, etc. *Int. Sci. Ser.*, 1882. Moggridge, *Harvesting Ants*, 1873. André, *Spec. gen. Hym.*, vi, 1896. Dalla Torre, *Catalogus Hymenopterorum*, Leipzig, 1892–6. de Saussure, *Monograph des Guêpes sociales*, Geneva, 1853–8. Forel, *Verh. Ges. deutsch. Naturf.*, lxvi, 1894, and *Ann. Soc. ent. Belgique*, xxxvii, 1893. Emery, *Zool. Jahrb. Syst.*, viii, 1896, p. 685. E. Saunders, *Hymenoptera Aculeata of the British Islands*, London, 1896.

head; the side-pieces of the prothorax overlap the prosternum. The antennae are as a rule simple. The mandibles remain conspicuous and are used for manipulating the wax and for many purposes other than eating. This is especially the case where a fluid pabulum is sucked up the "tongue," which is formed of the elongated first and second maxillae. The palp of the first maxilla is often rudimentary.

The number of visible segments in the abdomen varies from three to nine, and the abdomen in the female terminates in an ovipositor or sting which arises from outgrowths on the penultimate and ante-penultimate segments (Fig. 485). These outgrowths are by some regarded as homologous with true limbs. Amongst bees the legs take an active part in the collection of pollen. The wings are usually transparent and in the more typical forms a row of hooks on the anterior border of the posterior wing catch into a raised rim on the hinder edge of the fore-wing so that the two wings on each side are held together, and vibrate as a single membrane.

The tracheal system as in the *Diptera* is provided with vesicular swellings along each side of the abdomen. The nervous system tends to show a reduction of the number of ganglia and considerable concentration.

The larvae are eruciform and always have a distinct head. They are never quite so reduced as are some of the *Dipterous* maggots, but nevertheless the larvae of the



FIG. 486.—*a* Larva of a humble bee about to become a pupa; *b* pseudo-pupa (semi-pupa); *c* pupa (after Packard).

higher social forms are helpless, white, maggot-like creatures with no legs. The larvae of the saw-flies on the other hand are very like caterpillars and have several pairs of pro-legs in addition to the thoracic legs.

The appendages and the wings of the pupa are free. The latter either shut up in a cell by the parent, as in Bees, Wasps, etc., or protected by a cocoon formed by the larva.

Parthenogenesis is of wide occurrence in this Order, and in the *Cynipidae* it is accompanied by heterogamy, or alternation of

sexual and parthenogenetic reproduction. The result of parthenogenetic development is usually a male, but not unfrequently females only arise, and in some cases both sexes arise partheno-

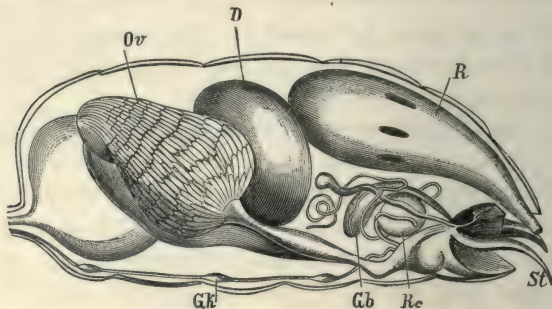


FIG. 487.—The viscera in the abdomen of the queen bee (after R. Leuckart). *D* alimentary canal; *R* rectum with rectal glands and anus; *Gk* chain of ganglia; *Ov* ovary; *Re* receptaculum seminis; *Gb* reservoir of poison gland; *St* sting.

genetically from the same brood (sawflies). The queen bee when fertilized stores the spermatozoa in a receptaculum seminis which she can open at will, and the view is generally held that if she closes this sac the unfertilized eggs then laid develop into males or drones, but that if she permit the access of spermatozoa to the eggs, females or workers arise.

Polymorphism is also a dominant feature in many of the colonial forms. Different castes are present, such as the worker, the drone, the soldier, the queen, and so on, and it is thought that these various castes are evoked by differences in the quality and amount of the food supplied to the larvae.*

The Hymenoptera form a very large order with some 30,000 described species. This figure will probably be multiplied by eight before the existing species are exhausted. They are divided into two sub-orders, the Sessiliventres and the Petiolata.

Sub-order 1. SESSILIVENTRES.†

Base of abdomen as broad as base of thorax or nearly so; no waist; first abdominal segment not completely fused with thorax; trochanter divided into

* There is unfortunately no space in this volume to devote to the fascinating habits and life histories of most of the Hymenoptera, but for graphic accounts of these the student is referred to Mr. Sharp's volumes in the Cambridge Natural History, and to the works of the eminent French naturalist, J. H. Fabre.

† P. Cameron, *Monograph Brit. Phytophagous Hymenoptera*, Ray Society, 1882-1893.

two; larvae with thoracic legs and usually with pro-legs; they live on plants. Female furnished at the extremity of the body with saws or boring apparatus, usually concealed.

Fam. 1. **Cephidæ**. Small, slender Insects with weak exoskeleton; dorsal sclerite between thorax and abdomen divided into two; the prothorax free and long; the anterior tibia bears one spine. The larvae of Stem-sawflies live in the stems of plants or on tender twigs. They are white and rather maggot-like and their thoracic legs are but feebly developed. The female bores a hole with her two saw-like ovipositors and deposits her eggs in the stem or twig; the larva when hatched eats its way along the stalk. In this manner *Cephus pygmaeus* does much harm to corn in Europe and *C. integer* destroys the younger shoots of the willow in America. About 100 species are known, chiefly from the Mediterranean area.

Fam. 2. **Oryssidæ**. Dorsal sclerite between thorax and abdomen not divided, antennae arising below the eyes, their bases overhung by a ridge. This family has but one genus *Oryssus*, with about twenty species of which one, *O. abietinus*, is British. The abdomen is closely fused with the thorax and has little or no independent movement.

Fam. 3. **Siricidæ**. Large and often brightly coloured insects. The anterior lobe of the mesonotum is in contact with the mesoscutellum and not separated by the intrusion of the lateral pieces; the first abdominal dorsal sclerite is divided. The female has a well developed boring appa-

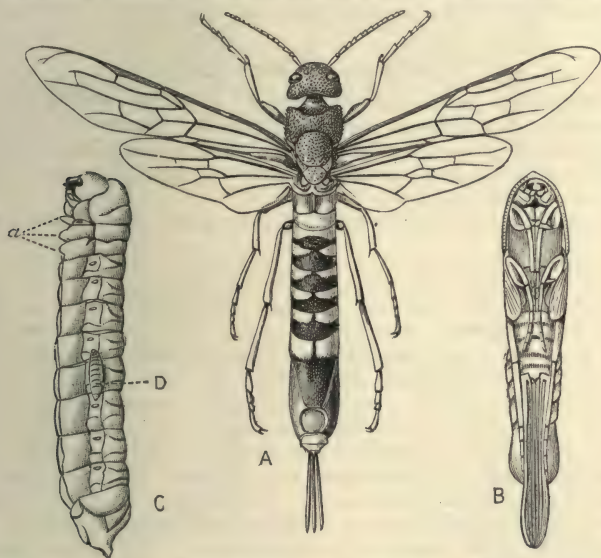


FIG. 488.—*Tremex columba*, North America. A Imago, female; B pupa, female, ventral aspect; C larva; a imperfect legs; D parasitic larva of *Thalessa* (p. 760). (B and D after Riley.)

tus. There are about a hundred species of Siricidæ and they are chiefly found amongst the forests of the Northern Hemisphere. The females by the aid of the powerful saw, which arises far forward on the ventral surface

of the abdomen, deposits her eggs in the standing timber, and the larvae do much damage by burrowing through the wood. Thus *Sirex gigas*, British, but much more common abroad, injures fir-trees. *S. juvenis* is rarer. *Tremex columba* (Fig. 488) is a well known North American species.

Fam. 4. **Tenthredinidae.** The anterior lobe of the mesonotum is separated from the mesoscutellum by the ingrowth of the lateral pieces; two spines on each anterior tibia; pronotum small and fused with mesonotum. The Saw-flies are insects with antennae of varying form, which may have as few as three segments or as many as forty. The well known ovipositor consists of a pair of plates toothed on the lower edge and file-like on the outer surface, protected by a pair of sheaths. This saw pierces into leaves and deposits an egg and a drop of some fluid. The egg is said to grow considerably after being laid. Many of the larvae feed on leaves, some mining in them, others forming galls. Most of the larvae resemble caterpillars in appearance, but they have usually more pro-legs and these appendages have no ring of hooks at the free end. One pair of pro-legs is always on the fifth segment of the body, and this segment in the Lepidoptera is invariably devoid of these structures. Some species have larvae covered with slime like a slug. Cocoons are usually formed, and often in the ground. *Athalia spinarum* injures turnips, *Nematus ribesii* currant and gooseberry bushes. *Hylotoma rosae* injures rose bushes. Many are parthenogenetic. The family is a large one with some two thousand species, which are most common in temperate climates. About four hundred are recorded from our country.

Sub-order 2. PETIOLATA.

Abdomen joined to the apparent thorax by a slender waist (petiole), and very movable. The apparent thorax is composed of the true thorax and of the first abdominal segment or propodeum, which is closely united therewith. The petiole is formed of the second, or second and third, abdominal segments. The larvae are white and legless.

This sub-order has been divided into three series of which the first is—

Series 1. PARASITICA.

Trochanter divided into two segments. Ovipositor present in female.

Fam. 5. **Cynipidae.** Small, dark insects with very few cells in the wings; pro- and meso-notum joined and pronotum extending back to insertion of fore-wings; antennae straight, with twelve to fifteen segments. The Gall-flies have usually a peculiar abdomen in which the tergum of the second or third segment is enlarged and covers in the succeeding segments. The ovipositor is long, coiled up in the body, and of great delicacy. The eggs are laid usually in plants where their presence, or that of some secretion, sets up the formation of a gall. In this gall when complete, or even in the bodies of the larvae living in it, other Cynipidae lay their eggs. A list of galls formed by this family is given by Cameron.* One of the commonest species is *Rhodites rosae* which forms the bedeguar gall on rose-bushes. Many forms are parthenogenetic, and indeed in several species the male is quite unknown. The family is cosmopolitan.

Fam. 6. **Proctotrypidae.** Few or no wing-nervures; pronotum as in

* *Ray Society*, iv, 1893; v. also Alder, *Alternating Generations*, Transl. by C. R. Straton, 1894.

preceding family; abdomen pointed behind and often bent downwards; ovipositor retractile but not coiled; larva parasitic. A large and variable, cosmopolitan family of small or minute insects difficult to define. The ovipositor is in all cases tubular. The trochanter in some cases remains undivided. Such larvae as are known live in the bodies or in the eggs of other insects or of spiders, and there they usually pupate. Some, e.g. the members of the sub-family



FIG. 489.—*Alaptus excisus*, Westwood. Britain. (Probable size about $\frac{1}{4}$ millim.) From Sharp.

Mymarinae, are aquatic and are said to lay their eggs in those of Dragon-

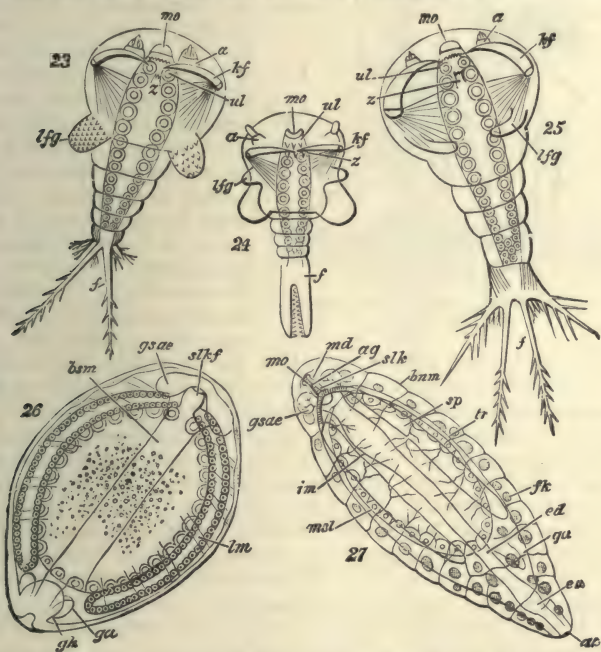


FIG. 490.—Stages in the development of *Platygaster* (after Ganin from Lubbock). 23, 24, 25, so-called *Cyclops*-like larvae of three species of *Platygaster*; 26 second larval stage; 27 third larval stage. *a* antenna; *ag* salivary duct; *ao* anus; *fk* fat-body; *ga* genital organs; *ing*; *ed* intestine; *ew* rectum; *f* furcal appendage; *fk* fat-body; *ga* genital organs; *gh* proctodaeum; *gsae* supra-oesophageal ganglion; *kf* hook-like feet; *lfg* lateral limbs; *lm*, *sp* salivary glands; *md* mandibles; *mo* mouth; *msl* stomach; *slk*, *slkf* oesophagus; *tr* tracheae; *ul* lower lip.

flies. Some again are dimorphic: the female *Scleroderma* is usually apterous; when wings are present ocelli always appear, though they are as a rule absent in wingless forms. *Platygaster* (Fig. 490) infests the larvae of *Cecidomyia* and helps to diminish the numbers of the Hessian-fly. Polyembryony exists in this and in the following family (v. p. 641). *Polynema natans* is a remarkable aquatic form which uses its wings for swimming and is an egg-parasite of dragon flies. *Alaptus* (Fig. 489) is one of the smallest insects known.

Fam. 7. Chalcididae. Pronotum partly free and not reaching back to the level of the wing-insertion. Antennae elbowed, of seven to thirteen segments. No cells in wings, but one stout nervure which runs at first parallel to, but finally falls into, the anterior border, after giving off a slight twig. Trochanters divided. The Chalcids form a very large but imperfectly known, clearly defined family of minute parasitic insects. Many



FIG. 491.—*Thalesa lunator*. Oviposition
(after Riley).

of their larvae live in galls preying on the more legitimate inhabitants. Sometimes the egg is laid in the caterpillars and even in the pupae of Lepidoptera and often in the bodies of Bees and Beetles. They help to keep down swarms of injurious insects, and cases are on record where they have destroyed 95 per cent. of the eggs of these enemies to cultivation. The numerous species known as fig-insects have frequently wingless males and winged females, an unusual arrangement. *Blas-tophaga grossorum* is the chief agent in the process of caprification, as the fertilization of the fig is called. The insects which live normally in the wild-fig are allowed access to the cultivated varieties. Unless the *Blas-*

phaga be present some writers think that the fig will be but imperfectly formed. Chalcids are often metallically coloured and of bizarre shapes. The larva usually pupates within the body of its host.

Fam. 8. Ichneumonidae. Long, straight, many segmented antennae; wings with many nervures and cells; the cubital cell of the fore-wing is separated from the second posterior by two cells. The trochanters are divided into two segments. The Ichneumon-flies deposit their eggs in the bodies of caterpillars and grubs by means of their long ovipositors; and myriads of insects are destroyed by ichneumon-larvae. The larvae are said to eat, at any rate at first, the less essential organs of their host, such as the fat body; but in some cases at least they seem to live chiefly on the fluids in their host's body. *Rhyssa* and *Thalesa* (Fig. 491) have ovipositors of great length, and pierce solid wood with them in order to lay their eggs in the burrows of the wood-boring larvae of the Siricidae (Fig. 488). The number of species is very great; over six thousand, about one-fifth of which are British, have been described. *Paniscus*.

Fam. 9. Braconidae. The cubital cell of the fore-wing separated from

the second posterior by one cell only. This family is closely allied to the preceding one, and is separated from it almost wholly by the presence of the single cell on the fore-wing just mentioned. The parasitic habits of the larvae are similar in the two families. The distribution of the two families is alike. The Braconidae contains a very large number of species many hundreds of which occur in this country.

Fam. 10. **Stephanidae**. Many segments (thirty to seventy) in the antennae; head spherical; wings with a costal cell; posterior femora usually toothed. An ill-defined family comprising two rare but widely-distributed forms *Stephanus* and *Stenophasmus*.

Fam. 11. **Megalyridae**. The abdomen is short and broad and the waist is wanting; female with a long ovipositor; antennae fourteen-segmented. This family includes only the rare, anomalous, Australian *Megalyra*.

Fam. 12. **Evanidae**. The waist or second abdominal segment is inserted on the dorsal aspect of the first or propodeum; antennae straight, with thirteen or fourteen segments; larvae parasitic. Another small family of three genera: *Evania* (whose larvae live in cockroach egg-cases), *Gasteruption* and *Aulacus* (whose larvae devour other Hymenopterous insects). The genera have a large number of species a few of which are British.

Fam. 13. **Pelecinidae**. Trochanter not divided; marked sexual dimorphism; the female has a very long abdomen, but no ovipositor. Again a family of three genera, *Ophionellus*, *Monomachus* and *Pelecinus*, the last named common in the warmer parts of America. The larvae are said to be parasitic in other insects.

Fam. 14. **Trigonidae**. The oval abdomen of five visible segments has no waist; antennae twenty-five segmented; trochanter partly divided; wings with many nervures. Another small family, whose chief genus *Trigonalys* is represented in Britain by one species.



FIG. 492.—*Chrysis ignita* ♀. England. From Sharp.

Series 2. TUBULIFERA.

Trochanter not divided; abdomen shows only three, four, or five segments; ovipositor transversely segmented and usually withdrawn into the body.

Fam. 15. **Chrysididae**. Bright, metallic insects with hard exoskeleton; antennae elbowed, with usually thirteen segments; the abdomen is concave below and can be bent forward under the thorax. This family is somewhat aberrant and may come near the Proctotrypidae. It contains the Ruby-wasps, which lay their eggs in bees' and wasps' nests, the Ruby-wasp

larvae eating up the larvae of the rightful owners, and sometimes, apparently, caterpillars stored up by the rightful owners as food for their larvae. The family is widely spread and has some hundreds of species, about twenty of which are British. They are brilliantly coloured and fly swiftly in hot, sunny places. *Chrysis* (Fig. 492), *Parnopes*, *Cleptes*.

Series 3. ACULEATA.

Trochanter as a rule not divided ; females (both perfect females and workers) with a sting, except in some ants ; antennae of females with twelve segments, of males with thirteen.

This series is mainly characterized by a change of function and structure in the ovipositor. This ceases to transmit the ova—these pass to the exterior at its base—and becomes a weapon of offence, the sting. The larvae are white grubs with no legs, and they live in cells provided for them by the imagines; until a late stage they are aproctous. The pupa is soft. The sting (Fig. 485) consists of a sheath, a director paired in its origin, and a pair of spicules or needles. The last segment but one of the abdomen bears in the late larva four papillae: of these the two inner form the director and the two outer the sheath. The segment next in front, the eighth abdominal, bears but one pair of papillae, and these form the spicules. The question of the homologies of these organs with abdominal limbs is a matter of dispute.* In the imago of the male sex the two last segments are tucked into the preceding segments; in the female three segments are thus hidden.

Fam. 16. **Apidae** (*Anthophila*). Some of the hairs clothing the body are feathered or plumose; the mouth parts are usually elongate; the proximal segment of the posterior foot is enlarged. The Apidae are often



FIG. 493.—*Apis mellifica*. a queen; b worker; c drone.

social, with a grade of infertile females known as workers. This family is of considerable size with some hundred and fifty genera and ten times as many species. In many cases the posterior legs, especially of the workers (Fig. 494), are highly modified to carry home the pollen which is kneaded into "bee-bread." The pollen may be simply entangled in the hairs or damped and moulded into pollen-plates. The proboscis may be short; but in the Hive-bee, Humble-bee and others the maxillae (both pairs) are drawn out, and in repose the proboscis lies with its distal parts doubled back along the ventral surface of the body. The ligula is said to be protruded by fluid forced into it from the general body-cavity. Bees absorb the nectar from flowers and store it in their crops until the time comes for them to regurgitate it as honey. During its stay in the crop

* v. Heymons, *Morph. Jahrb.*, xxiv, 1896, p. 178.

the cane-sugar of the nectar has become the grape-sugar of honey. The solitary bees store with food for the larva a single cell or several cells, which may be made of clay or hollowed out in wood. They then deposit one egg in each cell and seal it up, repeating the process later. A minute drop of the poison is injected into each cell before the latter is sealed. The formic acid which it contains acts as an antiseptic and prevents the fermentation of the sugar. The social forms also rear their young in cells, but these are massed together in large numbers and do not remain sealed up, the workers going round from time to time and feeding the larvae, just as warders feed the prisoners in a cellular prison. The wax of which these masses of cells or "combs" are made is secreted by glands situated on the inner face of the ventral plates of the abdominal segments. The wax appears in the form of thin plates which are removed by the hinder pair of legs and then "worked up" by the mandibles. Many species are parasitic in the hives of more industrious forms.

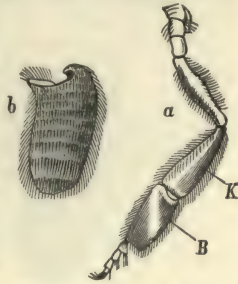


FIG. 494.—*a* hind leg of a worker of *Apis mellifica*; *K* basket on the tibia; *B* enlarged tarsal joint with brush on the under side; *b* brush, more strongly magnified.

Sub-fam. 1. **Archiapinae**. Proboscis short with concave-margined free end; very few hairs, but these are plumose; posterior legs unmodified. This archaic group includes the genus *Prosopis* (some add to it *Sphecodes*) which builds its nest in bramble-stems or crevices in walls. There are ten British species.

Sub-fam. 2. **Obtusilinguinae**. Hairy, with hairy second and third legs adapted for carrying pollen; ligula short and bilobed. *Colletes*, with six British species, digs holes in the ground and divides the burrow into a few cells which it fills with fluid food. *Sphecodes* seems to be a genus in a very plastic condition, for there is such variation in form as to make specific differences a matter of great difficulty. Its habits, sometimes industrial, sometimes parasitic, are equally lacking in precision and its position in any classification is uncertain.



FIG. 495.—*Sphecodes gibbus* ♀. Britain. From Sharp.

Sub-fam. 3. **Andreninae**. Ligula short, with acute tip; gregarious bees, the cells made by one individual connected by passages with those made by others. *Halictus* makes oval, underground cells lined with a varnish which is probably produced by the salivary glands. *Andrena* is a large genus with some fifty British species.

They live in sandy and gravelly soil. *Dasyпода* also burrows in loose earth, making tunnels of one or two feet in length.

Sub-fam. 4. **Denudatinae**. Parasitic and without any modifications for carrying pollen. The bees classed together here have little in common beyond their parasitic habits. *Stelis* lays its eggs in the

cells of *Osmia* or to the same end breaks open the cells of *Chalicodoma*, *Nomada* preys on *Andrena* and so on.

Sub-fam. 5. **Scopulipedinae.** Solitary, not parasitic bees, with long ligula. A rather unnatural group with four British genera *Anthophora*, *Ceratina*, *Eucera* and *Saropoda*. The first-named resembles *Bombus*; it often makes cavities in cliffs. *Xylocopa* is a carpenter bee and makes its cells in dry timber. *Euglossa*, a very fine form, has a proboscis much longer than its body.

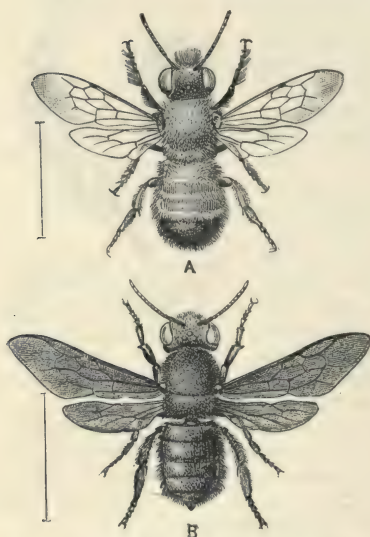


FIG. 496.—*Chalicodoma muraria*. Greece.
A male; B female. From Sharp.

whole with a dome-shaped covering. *Anthidium* makes cells of down and cotton collected from plants, and places them in such shelters as empty snail-shells or the cells of other Hymenoptera. *Osmia* also selects already formed shelters in timber, walls or banks. *Megachile* is the leaf cutting bee, and makes a series of cells in some small burrow out of pieces of plant-leaves which it neatly cuts and places. There are four British genera.

Sub-fam. 7. **Socialinae.** Social bees, which form colonies, with different grades of females. In *Bombus* the workers are not externally clearly differentiated from the queens, and in the autumn each community perishes, save for a few females which survive the winter, and each of which acts as a queen and starts a new colony in the spring. The waxy cells are piled together irregularly in some hollow in the ground or in a bank, and a well-filled community contains only some few hundred bees, in some species even fewer. The wax is secreted



FIG. 497.—*Osmia tricornis* ♀. Algeria.
From Sharp.

by the abdomen and transferred to the legs before being kneaded into the building material.* *Psithyrus* lives in the nests of Humble-bees (*Bombus*), and the several species curiously resemble the species on which they quarter themselves. *Melipona* is the Mosquito-bee and very small in size; it has a stunted form of sting, but does not use it for offence. There seems to be one queen in each nest and the very numerous inhabitants are said to swarm occasionally. *Apis mellifica* is the Honey-bee (Fig. 493). Here the drones (males), the workers (infertile females) and the queens are structurally different, and form colonies that persist from year to year. New communities arise by swarming. A new queen-bee having been reared, the queen-mother with some adherents quits the hive and establishes a new one. The cell for the royal larva is bigger than that for the larval drones and workers, and the larval queen enjoys a special diet. The drones are said to arise from unfertilized eggs. The queen-bee has a longer abdomen than the worker; she forms no wax and has no transverse row of hairs on the enlarged first tarsal segment for the gathering of pollen. The male or drone is broader and stouter, with larger eyes which meet above; and the hind-legs are unmodified for collecting pollen. The Honey-bee has been domesticated for so long a period that many local races have arisen.

The division of labour which plays such a prominent part in the economy of the higher Hymenoptera reaches the highest pitch amongst the bees. The queen-bee, in the case of *Apis mellifica*, alone, lays eggs, sometimes at the rate of 3,000 a day; she and the workers live through the winter, but the drones all perish in the autumn. The drones do no work in the hive; they arise from unfertilized eggs and are killed in the autumn (slaughter of drones). During the winter the queen-bee and the workers live upon the food stored up in the hive; when spring returns she deposits eggs, first in the cells of the workers and then of the drones. After a time certain large royal cells are constructed, and in each of these she lays a fertilized egg; the larvae which proceed from these eggs receive a richer nourishment and become queens. The drones take twenty-four days to develop, the workers twenty, and the queens sixteen. Before the eldest of the royal pupae gives rise to a queen in the imaginal state, the queen mother with a number of the workers leave the hive (first swarm). Thus a new colony arises. The young queen either kills all the other royal larvae and remains in the old hive, or if she is prevented from doing this by the workers and the population is still large enough, she also leaves the old hive with a part of the workers (second swarm or cast) before the appearance of a second queen. Soon after the metamorphosis is complete the queen is fertilized by a drone whilst flying in the air. The drone immediately dies, and the queen, which has only been fertilized once, can continue to lay fertilized ova for several years. If the wings of the queen are paralysed and she is unable to copulate,

* Cf. Titania:—

The honey-bags steal from the humble-bees,
And for night-tapers crop their waxen thighs,
And light them at the fiery glow-worm's eyes.

A Midsummer Night's Dream,
Act III, scene 1, lines 154-156.

she lays eggs which only give rise to drones ; the same is the case with the fertilized queen in her old age when the contents of the receptaculum seminis are exhausted. Workers may also lay eggs which develop into drones ; the larvae destined to become workers may, if the food-supply at an early stage be abundant, become queens. A hive may number as many as twenty to thirty thousand individuals, of which the drones do not form more than one per cent.

The following three families comprise the true Wasps. They are sometimes classed together in a group, the *Diploptera*, characterized by the anterior wings being longitudinally plicate in repose, the pronotum reaching to the tegulae, and the posterior tarsi not being modified for industrial purposes.

Fam. 17. **Eumenidae.** Solitary wasps. Tarsal claws toothed or bifid ; one spur only on the second pair of tibiae ; no workers and no communities. A diverse group of some eight hundred species, sixteen of which occur

in Britain.

Eumenes constructs a clay-cell and stores it with caterpillars, perhaps partially paralysed by her sting. *Odynerus* uses hollows in walls, wood, etc. *Rhygchium* forms cells in plant-stems.

Fam. 18.

Vespidae. Tarsal claws simple ; two spurs on the



FIG. 498.—*Odynerus antilope* ♀. Britain. From Sharp.

second pair of tibiae ; workers present ; they live in communities in papery nests. Wasps' nests are built of small vegetable fragments, often taken from decayed wood, which are chewed up by the mandibles till they become almost like coarse paper. The combs are usually in layers, each hanging by little pillars from the layer above, and the whole surrounded by an outer envelope. The workers, which are not structurally different from the queens (perfect females), may occasionally lay eggs which are probably fertilized. The colonies are annual, existing for the summer only. In the autumn all die, with the exception of a few fertilized females, which creep into crevices of trees or under stones, and hibernate throughout the winter. In the spring the female emerges and commences to build a nest. As soon as two or three cells are finished the female lays an egg in each, and when the white apodous grubs hatch out they have to be fed, whilst at the same time the mother is widening and deepening their cells and adding others.

The larval stage lasts about two weeks, and then the grubs cease to eat and turn to pupae in their cells. The imago emerges in ten days, and sets to work to enlarge the nest. As soon as the perfect insect vacates its cell, this is cleaned out and another egg is deposited in it.

During the first half of the summer, only workers appear, but later males and perfect females make their appearance, the former perhaps from the parthenogenetic eggs of the later brood of workers; all these kinds are winged, but the workers are smaller than the males or females. The sexes pair whilst flying, and soon afterwards the males die. The youngest larvae are fed on nectar from plants, but this diet is soon replaced by one of insect flesh, the female wasp catching her insect prey on the wing. This is slightly masticated by the mandibles and then offered to the progeny.

Of the eight British species, all of them belonging to the genus *Vespa*, *V. germanica*, *V. rufa* and *V. vulgaris* make their nests underground, *V. arborea*, *V. sylvestris* and *V. norvegica* in trees; *V. crabro*, the Hornet, in some such retreat as the hollow of a tree, whilst *V. austriaca* lives in the nests of other species. The hornet does not extend north of the Midlands. *Polistes* is the largest genus.

Fam. 19. **Masariidae** (Fig. 499). Claws toothed; fore-wings with two sub-marginal cells—the last two families have four; antennae clubbed. A small family of few and rare forms. *Masaris*, *Ceramius* and others are Mediterranean, *Paragia* Australian and *Trimeria* S. American. They seem mostly to construct earthen cells either underground or on twigs.

The following three families are often united under the name Fossores or Digging Wasps. The anterior wing is not plicate in repose; the hairs are not plumose; the basal segments of the abdomen have dorsally no prominences; there is no worker caste.

Fam. 20. **Scoliidae**. The sides of the pronotum reach to the tegulae at the base of the wings; abdomen with a chink between the first two segments on the ventral side. This family includes five sub-families consisting chiefly of tropical forms. They neither construct cells nor burrows, but as a rule lay their eggs on some insect larva which they have previously paralysed with their sting, and which serves their larvae for food.

Sub-fam. 1. **Mutillinae**. No wings or ocelli in the females, in which also the parts of the thorax are closely fused; the males are winged, with ocelli and parts of the thorax distinct; two spurs on second pair of tibiae; two or three sub-marginal cells on fore-wing.

This sub-family is rather ant-like and the members are known as "Solitary Ants"; the hairy coating and the absence of a node at the base of the abdomen however readily distinguish them from true ants. Many of them are brightly coloured, black, red, yellow and white occurring, and some stridulate. The larvae live at the expense

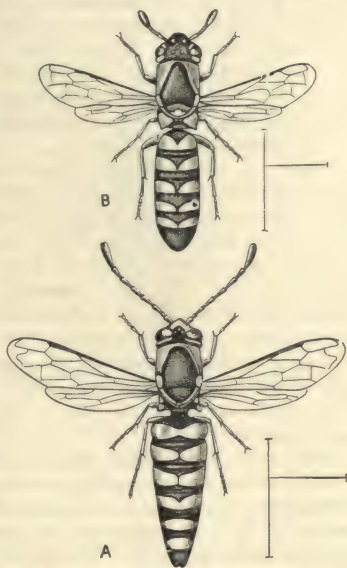


FIG. 499.—*Masaris vespiiformis*. A male; B female. Egypt (after Schaum).

of various Aculeate Hymenoptera, *Mutilla europaea* in the nests of *Bombus*. Three species are British but rare.

Sub-fam. 2. **Thynninae**. Males winged, females wingless; in the latter the thorax is divided into three sub-equal parts; no constriction between the second and third abdominal segments; wing nervures reach the edge of wing. This sub-family is also ant-like, the single and rare British species *Methoca ichneumonides* being often taken for an ant. Their most striking feature is the extreme difference between the two sexes.

Sub-fam. 3. **Scoliinae**. One apical spur on second tibiae; both sexes winged; wing nervures do not reach edge of wing; legs stout. This sub-family includes many large and hairy forms, the females usually larger than the males. They generally lay their eggs in such larvae of Lamellicorn beetles as burrow in the ground, e.g. *Scolia bifasciata* in the larvae of *Cetonia*. The group is largely tropical.

Sub-fam. 4. **Sapyginae**. Slender legs and antennae, abdomen not ending in spines. The single genus *Sapyga* lays its eggs in bees' nests, e.g. those of *Osmia*, and its larva devours the food laid up for the young. Two species occur in Britain.

Sub-fam. 5. **Rhopalosominae**. Antennae long and spiny; ocelli very large; tarsi peculiar, claws bifid. A single genus *Rhopalosoma* of unknown habits.

Fam. 21. **Pompilidae**. Pronotum reaches base of wing; no constriction between second and third abdominal segments; posterior legs long; eyes elliptical and not crescentiform. A very large family of wasps which dig nests in banks, etc., and store them with the paralysed bodies of spiders or more rarely of insects. In this way *Pompilus* and *Calicurgus* destroy large numbers of spiders, usually of the more voracious kinds. These wasps are active walkers and generally drag their victims to their lair along the ground. It is characteristic of many Pompilidae to run swiftly along the ground, with quivering wings and vibrating antennae. Some species are very large. *Pepsis* frequently attains a length of two inches and can overcome spiders as big as the Tarantula. The family is widely distributed.

Fam. 22. **Sphegidae**. Pronotum short and not reaching to base of wings; when the stigmatic lobes reach to the level of the insertion of the wings, they are below and separated from the place of insertion. This very large family is probably not a natural assemblage; it is divided into ten sub-families:—

Sub-fam. 1. **Spheginae**. Abdomen with a slender pedicel; two spurs on the second tibiae. A large group with *Sphex* as the chief genus. It burrows in the ground and stores its cells with the paralysed bodies of crickets, grass-hoppers and locusts. *Ammophila* uses caterpillars for the same purpose. *Pelopaesus* usually makes its home in human dwellings and stores its larder with spiders.

Sub-fam. 2. **Ampulicinae**. Prothorax elongate, produced into a neck in front; clypeus beak-like; four submarginal cells; metathorax long and ventrally split to permit of the forward flexure of the abdomen. A widely distributed sub-family with few species and few individuals. They feed on cockroaches. *Ampulex* forms no nests.

Sub-fam. 3. **Larrinae**. No pedicel or at most a very short one, the second tibiae have but one spur; marginal cell of fore-wing appendiculate, i.e. with a second cell more or less completely marked

off; labrum small. The well-known genus *Tachytes* has habits very similar to those of *Spheex*, some species preying on *Mantis*. *Larra* stores up mole-crickets; others grass-hoppers.

Sub-fam. 4. **Trypoxyloninae**. Marginal cell not appendiculate; eyes concave on inner surface. *Trypoxylon* builds clay nests often near human dwellings, and stores them with spiders; the second genus is *Pison*.

Sub-fam. 5. **Astatinae**. The eyes in the male meet in the middle dorsal line; two spurs on the second tibiae. This sub-family has but one genus *Astata* (some authorities however add *Oxybelus*). Two species are British, one of which provisions its underground cell with the Hemipteron *Pentatoma*.

Sub-fam. 6. **Bembecinae**. Marginal cell not appendiculate; nervures nearly reach to edge of wing; no pedicel; abdomen heavy; labrum often elongated. The members of the genus *Bembex* (Fig. 500) feed their young mainly on Diptera, which they kill and carry to their cells between their legs. As the insects are killed, they must frequently be replaced by new victims, and the parent is kept busy supplying the young with fresh food. For the most part the cells are formed in sandy banks and the entrance is blocked except when in use.

Sub-fam. 7. **Nyssoninae**. Labrum short; no pedicel; marginal cells not appendiculate. An ill-defined group, many of its members having a divided trochanter something like that of the Parasitica.

Mellinus catches flies, feigning death as it lies in wait for them.

Sub-fam. 8. **Philanthinae**. Three complete sub-marginal cells on anterior wing; labrum not elongate; anterior part of abdomen constricted but without a slender pedicel. Wasp-like Fossores. *Cerceris* stores paralysed small bees and beetles, and the different species attack different forms of Coleoptera. *Philanthus* kills honey-bees both for its own food and that of the larvae, which are carefully fed at intervals with fresh food.

Sub-fam. 9. **Mimesinae**. A non-cylindrical pedicel present; one spur on the second tibiae; marginal cells two or three. This family (including the Pempredoninae) comprises a few not very well known insects. *Psen* and *Passaloecus* make their cells in hollow stems, *Pempredon lugubris* in decayed beech wood. They store up Psyllidae and Aphidae.

Sub-fam. 10. **Crabroninae**. One sub-marginal and two discoidal cells; abdomen rarely pedicellate; pronotum short. These are small, rather wasp-like insects with large, square heads. They are the commonest of our digging-wasps, *Crabro* having over thirty British species. They mostly form their cells in dead wood or in stems, and store them with Diptera.



FIG. 500.—*Bembex rosstrata* ♂. Europe. From Sharp.

Fam. 23. **Formicidae.** The second, and sometimes also the third, abdominal segment is constricted fore and aft, so as to form an often irregular "bead" or node; the fourth segment usually very large; the trochanters are not divided; the proximal segment in the antennae elongate, the two forming a scape which bears at an angle a flagellum of eight to eleven segments. This large and diverse family of social insects comprises the Ants. Their mouth is so arranged that the labrum and labium come together and close it between the mandibles, which with the palps lie as it were outside, and to the side of, the mouth. The mandibles can be shut down and firmly locked together over the already closed mouth. The size of the head varies greatly, and even in the same species the workers may have small heads or large heads; in the latter case they are called soldiers. The stridulating organs by means of which ants seem to communicate with one another, are usually connected with the complex articulation of the base of the abdomen. Ants are active walkers and their legs are long. As a rule, the males are smaller than the

females. They live in communities, which comprise, besides the winged males and females, a number of wingless workers or neuters. These are in reality aborted females, and, like the functional individuals of that sex, are provided with poison glands. The poison consists of formic acid, which is either injected by the sting into wounds, or is ejected, in which case it may get

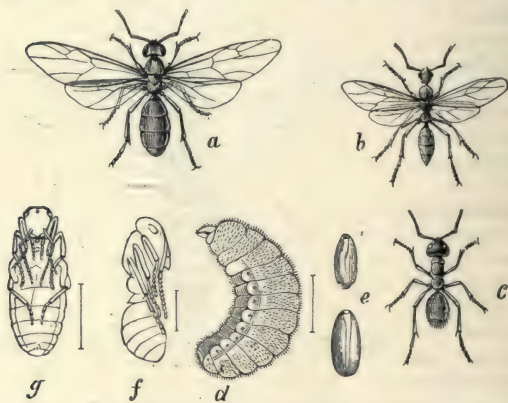


FIG. 501.—*Formica* (*Camponotus*) *herculeana*. *a* female; *b* male; *c* worker; *d* larva of *Formica rufa*; *e* pupa with case, so-called ant egg. *f*, *g* pupa liberated from the case.

into wounds made by the mandibles. Some of the workers, as is the case in the Termites, are specialized as "soldiers" with very formidable jaws and large heads. These defend the ant-hills when they are attacked. The workers survive the whole year, hibernating in cold climates during the winter months. Some of the reproducing females also hibernate, but the great number of both males and females live for a short time only, during the summer. No food is stored up in the ant-nest or "formicarium" for winter consumption, and those individuals which persist through the cold weather become torpid and cease to feed. With the return of spring the females which have survived lay eggs, and these, or in some species the eggs and larvae of the preceding autumn which have lasted through the winter, develop into a new brood, producing males, females and workers. The sexes pair whilst flying through the air; the males then die, the females cast their wings and either start off to form a new colony or are led back by the workers to the old. After casting their wings the muscles of flight—by far the largest in the body—

undergo a histolysis and are replaced by adipocytes.* The ants live upon both animal and vegetable substances, and are very fond of sweet things.

The real eggs are very small. The structures commonly called ants' eggs are the white, oval cocoons (case made by the larva).

The eggs, which are laid in nests by one or more queens, give rise to helpless larvae which are nursed and fed by workers. They are carried from one part of the nest to another when occasion requires, and unlike the Bees and Wasps they do not pass through their larval life in one cell or chamber. They are fed from the mouths of the workers, with semi-digested food. Some species form cocoons; in others the pupae are exposed. The pupae develop either into wingless forms, the workers and soldiers, or into winged forms, the males and fertile females. The queens are known to live several years.

The nests of ants are not definite in shape nor are they formed largely of wax or papery wood, but are irregular chambers connected by galleries and usually subterranean. Some species form chambers in timber; others inhabit spaces in plants, which they are said to defend from the attacks of leaf-cutting insects, etc.

Some two thousand species are recognized.

Sub-fam. 1. **Camponotinae.** The pedicel consists of one node;

poison gland a cushion of convolutions underlying a modified sting, which is simply an ejaculatory orifice for the poisonous fluid. This family comprises the so-called stingless ants, but though they do not sting they can eject a very poisonous fluid a considerable distance. There are some eight hundred species; *Camponotus* is by far the largest genus. In some cases, at any rate, when a new community is being started, a single female performs alone all the duties of the nest. After the first individuals, which are workers, have emerged, she becomes a true queen, performing no function except egg-laying; all other duties devolving henceforth upon the workers. In the large nests of the red-ant, *Formica rufa*, many beetles and one or two other ants live peacefully. *F. sanguinea*, British, makes slaves and servants of *F. fusca* and *F. cunicularia*; this habit is however carried to a

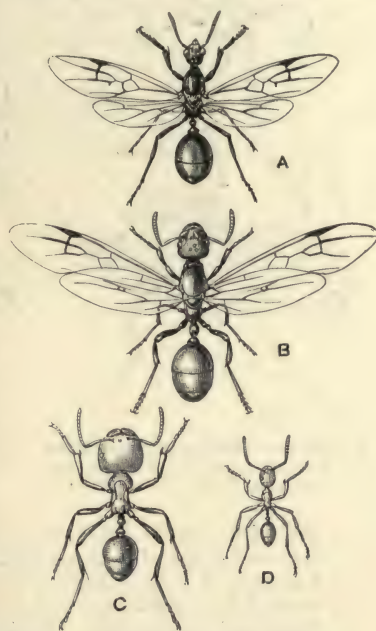


FIG. 502.—*Aphaenogaster (Messor) barbarus*. Algeria. A male; B female winged; C large worker or soldier; D small worker. $\times \frac{2}{3}$. From Sharp.

* C. Janet, C. R. Paris, cxliv, 1907, p. 393.

much greater extent by the genus *Polyergus*. *Lasius* is perhaps our commonest British genus.

Sub-fam. 2. **Dolichoderinae**. Like the previous family, but the poison sac does not form a cushion and there is a rudimentary sting. A small sub-family with few European representatives. *Tapinoma*, British, but rare, attends the fights of other ants and carries off and eats the vanquished.

Sub-fam. 3. **Myrmicinae**. Pedicel of two nodes; sting usually present. This sub-family includes some thousand species. It is often divided into four or even eight groups dependent on the shape of the head and its component parts. Many genera do not construct nests but live in the colonies of other ants, and some of these genera have undergone marked changes of structure. About ten species are British, the best known being *Myrmica rubra*. The harvesting ants of the genus *Aphaenogaster* (Fig. 502) of Europe and America store up

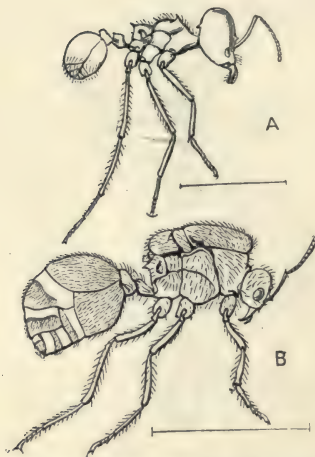


FIG. 503.—*Oecodoma cephalotes*. South America. A worker; B female after casting the wings. From Sharp.

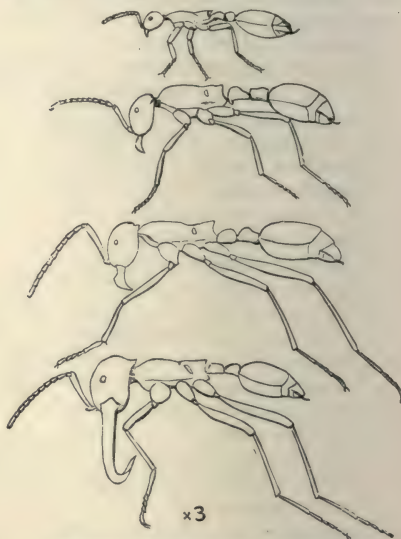


FIG. 504.—Various forms of worker of *Eciton hamatum*. Guatemala. From Sharp.

granaries of grain and seeds in their homes. *Atta* (*Oecodoma*) is the leaf-cutting ant of America (Fig. 503), and does much harm by denuding trees of their foliage. The leaves are carried to the nests and worked into balls, upon which the ants grow a certain fungus which forms their staple diet. *Pseudomyrma* lives in the bull's-horn thorn (an *Acacia*) and feeds on the secretions of certain glands in the leaves. *Cryptocerus* (Fig. 369).

Sub-fam. 4. **Ponerinae**. Pedicel of one node, abdomen elongated and loosely jointed between the first and second normal segments. A stridulating organ is often present between the loosely articulated segments just mentioned. Sting present. The family has some four hundred species, and is widely distributed but little known. Its col-

onies seem small. *Ponera contracta* and *P. punctatissima* are the sole British representatives. The latter is peculiar in that it has two kinds of male, one winged and one wingless. *Myrmecia*, the bull-dog ant of Australia, forms great mounds of earth.

Sub-fam. 5. **Dorylinae.** Clypeus minute and antennae arising close to front edge of head; abdomen drawn out, more or less cylindrical; pedicel imperfect, occasionally consisting of two nodes in the workers; the several castes very different; the females and workers often wholly blind, or at any rate without faceted eyes. This sub-family includes certain wandering ants which retain their social distinctions though they have no permanent home. *Eciton* (Fig. 504) is a well-known American genus which makes temporary shelters in hollows in trees, the members of the community massing together like a swarm of bees. But they have no abiding resting-place, and often leave their shelter on marauding expeditions and do not return. The genus formerly known as *Labidus* is now regarded as the male *Eciton*. *Dorylus* closely resembles this last-named form; but the female, formerly classed in a separate genus, in some forms is enormously enlarged, somewhat as in the Termites; the workers are blind but predaceous, and the communities rove.

Sub-fam. 6. **Amblyoponinae.** No true pedicel; the articulation between the second and third abdominal segments is broad. This group has relations with the Scolidae as well as with the Formicidae. *Amblyopone* and *Stigmatomma* are thought to be subterranean and social, but little is known of their habits. Both sexes are winged and the workers are nearly blind.

CHAPTER IX

CLASS V. ARACHNIDA*

This is a much more diverse Class † than the Insecta, and contains animals which vary within as wide limits as do those included in the class Crustacea. Many of the Orders are small, but the Spiders and Mites comprise a very large number of species, and in some species a very large number of individuals.

There are no antennae. The chelicerae are the first pair of appendages and the pedipalpi the second. The mouth lies between the bases of the pedipalps. In the more typical Orders a varying number of appendages starting from the third or the pedipalpi have at their proximal ends processes, called gnathobases, which project inward round the mouth and help to hold and break up the food.

In some divisions of the Arachnida the number of segments is definite as is the case with the Malacostraca. These segments are grouped into tagmata or categories of a higher order, and there are

* Pickard Cambridge, *Encyclopaedia Britannica*, ix Ed., 1872, Article *Arachnida*. E. R. Lankester, *ibid.*, x Ed., and The Structure and Classification of the Arachnida, *Quart. J. Micr. Sc.*, xlviii, 1905, p. 165. Hensen, Organs and Characters in Different Orders of Arachnida, *Entomol. Meddel*, iv, p. 137. G. Newport, Nervous and Circulatory Systems in Myriapoda and Macrurous Arachnids, *Phil. Trans.*, 1843. Claus, Degeneration in the Acari and Classification of Arthropoda, *Anz. Ak. Wiss.*, 1855, and *Ann. Nat. Hist* (5), xvii, 1886, p. 364, and xix, p. 225. Blanchard, Les Arachnides, in *L'Organisation du règne animal*. Gaubert, Recherches sur les Arachnides, *Ann. Sci. Nat.* (7), xiii, 1892. C. Koch, *Die Arachniden*, 16 vols., Nuremberg, 1831-48. Koch, Keyserling and Sörensen, *Die Arachniden Australiens*, Nuremberg, 1871-90. R. I. Pocock, Arachnida of British India and "On African Arachnida," *Proc. Zool. Soc.* and *Ann. Nat. Hist.*, 1867-1900. Simon, *Les Arachnides de la France*, 7 vols., Paris, 1874-81. *Hist. Nat. des Araignées*, 2 vols., Paris, 1892-6. Thorell, Arachnida from the Oriental Region, *Ann. Mus. Genova*, 1877-99.

† We differ from Lankester in regarding the Trilobites as more nearly allied to the Crustacea, especially to the Phyllopoda than to the Arachnids. As we do not include them here our group Arachnida is equivalent to his group the Nomeristica. E. R. Lankester, *Quart. J. Micr. Sci.*, xlviii, 1905, p. 165.

usually in a typical form three of these. Of these the *prosoma* or *cephalothorax* comprises all the segments in front of the segment bearing the genital pore. The region of body (*abdomen*) behind this sometimes falls into two parts, the *mesosoma* and the *metasoma*, but the position of the division between these two parts is not constant. These i.e. the *mesosoma* and the *metasoma* form the *opisthosoma* or the *abdomen* of authors. As stated in Chapter IV (p. 323)* there are in the embryos of spiders indications of a pair of somites in front of the cheliceral somites, and in this region vestigial antennae have been found in a spider (*Lycosa* sp.).† Between the *prosoma* and *mesosoma* embryology has shown that another segment exists for a time but disappears. It is impossible to say with certainty whether this pregenital segment belongs to the *prosoma* or to the *mesosoma*, but here we have reckoned it as belonging to the *prosoma*. Counting the pre-cheliceral embryonic somite found in spiders, we thus have the following scheme of segments in *Scorpio* or *Limulus* named after the appendages they bear:—

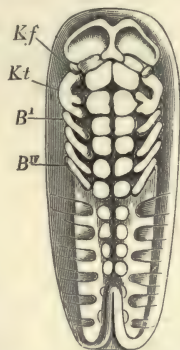


FIG. 505.—Embryo of a Scorpion (after E. Metschnikoff). *Kf* Chelicerae; *Kt* pedipalpi; *B¹* to *B⁴*, the four pairs of thoracic legs. There are rudimentary limbs on the abdomen, but the pregenital segment is not shown.

- | | | |
|---------------------------------------|-----------|------------|
| 1. Eyes or prechelicerae (see above). | Preoral† | } Prosoma. |
| 2. Chelicerae. | Preoral | |
| 3. Pedipalpi. | Paroral | |
| 4. 1st pair walking legs. | Postoral | |
| 5. 2nd " " " | " " | |
| 6. 3rd " " " | " " | |
| 7. 4th " " " | " " | |
| 8. Chilaria or Pregenital segment | | |

* G. H. Carpenter, *Quart. J. Mic. Sci.*, xlix, 1906, p. 469.

† Javovsky, *Zool. Anz.*, xiv, 1891–2.

‡ According to the view embodied in the table on p. 325 the chelicerae is reckoned as belonging to the second segment. In Chapter IV the eyes are not regarded as appendages

§ The remaining segments are of course postoral.

|| The appendages of this segment disappear in all Arachnids except in the Merostomata and Pycnogonida.

arisen independently in evolution. Whether this view is correct or not, it is worth noting that organs, which closely resemble tracheae and appear to have the same function, are found in certain terrestrial Isopods (p. 482) and in certain Siphonophora (vol. i, pp. 142-43). Finally, in some of the forms, usually degenerate both in their size and in the absence of heart and in reduced segmentation from parasitism or from some other cause, the tracheae disappear altogether and the respiration is entirely cutaneous.*

The heart is contained in a pericardium and consists of a certain number of chambers, in spiders and Phalangids three, in scorpions seven and in *Limulus* eight, indicated by the ostia. The circulation is largely lacunar, and, as is the rule in Arthropods, the chief spaces of the body are haemocoelic. Nevertheless in *Limulus* and in the scorpions both arteries and veins are well developed, and these animals have a far more definite system of blood-vessels than have any other Arthropod. In the first named genus and to a lesser extent in the scorpions the great ganglionic mass and the nerves which issue from it are sunk in or are invested by the arteries so that the nerves are described as being in the arteries. In the same two groups the walls of the pericardium are fibrous and complete, the blood returning to its cavity by paired veins which come from the respiratory organs. The blood before passing to the gill-books or lung-books is collected in a large median ventral sinus and Lankester has shown that the upper wall of this ventral sinus and the lower wall of the pericardium are connected by a series of paired, vertical muscles, seven pairs in *Scorpio* and eight in *Limulus*. The contraction of these muscles brings about the enlargement of the

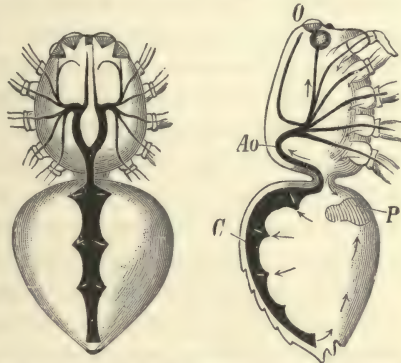


FIG. 506.—Heart and vascular trunks of *Lycosa*, in lateral and dorsal view (after Claparède). *P* Lungs; *C* heart; *Ao* aorta; *O* eyes.

* A similar disappearance of specialized respiratory organs occurs in the abbranchiate Urodeles, v. vol. ii, p. 278.

cavities of these two sinuses and a consequent inrush of blood into both.

The alimentary canal runs comparatively straight from the mouth to the anus and is devoid of convolutions. Many Arachnids live on animal and vegetable juices and in these the mouth is minute and a sucking pharynx, whose walls are divaricated by extrinsic muscles, lies close within it. The alimentary canal is different from that of the Crustacea since it gives off as a rule more than one pair of digestive glands. The glands, of which the anterior or prosomatic in the scorpion are termed salivary, secrete a fluid which is believed to act like the pancreatic fluid of vertebrates. The gastric glands are tubular in spiders and are bent into the bases of the limbs. Their distal ends are said to fuse in some species. They extend almost to the tip of some of the limbs in the Pantopoda. There seems no doubt that the food finds its way into the lumen of these glands and that a large part of the digestion goes on in them and not in the cavity of the alimentary canal. The proctodaeum varies in size; malpighian tubules (absent in *Limulus*) are one pair or more numerous; they open, as a rule, into the anterior end of the hind-gut, which bears in the spiders an enlargement termed the stercoral pocket in which the faeces accumulate. The anus is not quite terminal and is always slightly ventral. It may be succeeded by the sting as in scorpions or by a spine as in *Limulus*.

The excretion of waste nitrogenous matter is not confined to the above-mentioned malpighian tubules. Coxal glands are also present and are homologous with the green glands and shell glands of Crustacea. They are tubular portions of the coelom which open to the exterior. The opening in the Arachnida is minute and for long it escaped observation; in scorpions it is on the hinder face of the 3rd pair of legs, in *Limulus* the gland gives off a lobe into the 2nd, 3rd, 4th, and 5th legs and opens on the coxa of the 5th. In *Atypus*, one of the Araneina, it opens both in the base of the first and third pair of legs.

The internal skeleton or endosternite is cartilaginous in texture but yields chitin instead of chondrin or gelatine. This chitinous plate, which in *Limulus* "floats" between the prosomatic nerve mass and the alimentary canal, and in the scorpions forms a kind of diaphragm between the cavities of

the pro- and meso-soma, occurs again in spiders, and is much more highly developed in the Arachnida than in *Apus* or in the Decapoda, where only an insignificant plate occurs. Numerous muscles are attached to the endosternite.

The nervous system consists of a supra-oesophageal ganglion which supplies the eyes and the chelicerae, that is the appendages (if the eyes are appendages) of the preoral segments, the two prosthomeres of Lankester's terminology. The nerve ganglia of the postoral segments have in the Acarina, the Pedipalpi, the Solifugae and the Araneina fused into a central mass, though in the last named group the nerve which runs posteriorly to supply the abdomen bears a ganglion close to the base of the latter. In *Limulus* the circumoesophageal collar is very large and gives off nerves to the pedipalps and the remaining prosomatic appendages as well as to the genital opercula. The right and left halves of this collar are connected by a ladder-like series of transverse commissures; behind the collar the ventral cord gives off five nerves to the gill-books and is continued back to supply the metasoma and spine. In scorpions the nervous system is less concentrated and the ventral cord has seven discrete ganglia the first of which corresponds with the segment bearing the 3rd lung-book and the last with the 4th metasomatic segment. The nerves to the chelicerae and remaining appendages, up to and including the 2nd lung-book, arise from the collar or from the sub-oesophageal ganglion. The right and left halves of the ventral cord remain distinct throughout its course.

The chief sense organs are eyes which vary in number from two, in Acarines and Tardigrades, to twelve. Their grouping is often of systematic importance. Some mites are blind. Auditory organs, which may be presumed to exist in those Arachnids such as the scorpions and spiders which have stridulating organs, are apparently represented by sensory hairs usually on the pedipalps or on the walking limbs.

Arachnids are dioecious, but as a rule there is little external differentiation of sex except amongst the spiders, where the male is often much smaller than the female, and amongst some mites. The Phalangids possess a large extrusible ovipositor and penis and in the spiders the pedipalps are curiously modified and used in depositing the spermatozoa in the female orifice.

The reproductive organs with the ducts frequently form a ring, sometimes a network, which encircles the alimentary canal and nervous system.

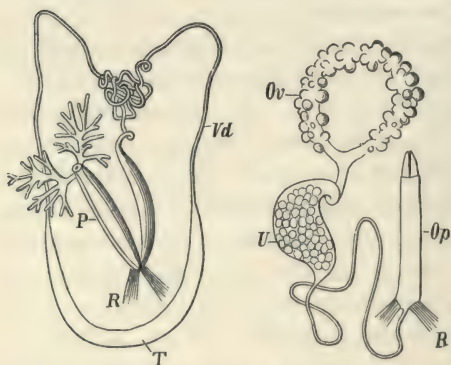


FIG. 507.—Male and female generative organs of *Phalangium opilio* (after Krohn). *T* Testis; *Vd* vasa deferentia; *P* penis with accessory glands; *R* retractor muscles; *Ov* ovary; *U* uterus; *Op* ovipositor.

The oviducts and vasa deferentia unite to open by a single, median, ventral pore, except in *Limulus*, which has paired pores. The ring-like ovary and testis of the Acarines and Phalangids have become in the scorpions and in *Limulus* retiform and lie embedded among the digestive glands. Receptacula

seminis and vesiculae seminales are usually swellings on the ducts, but in spiders the former are distinct from the oviducts and open just in front of the female opening. Accessory glands are also usually present but their exact function is still obscure.

The Pedipalps and scorpions and some mites are viviparous, the ova developing in the ovary or uterus. Many spiders and Pseudoscorpions attach their eggs to their bodies. As a rule the young are miniatures of their parents, but mites are often hatched with but three pairs of walking limbs and pass through a series of stages, separated by a moult, before becoming adult. The Phalangids die down during the winter and the race is then represented only by developing eggs.

Certain Acarines are parasitic on plants and on animals, and some of them as well as some spiders are aquatic, but the great majority of Arachnids are terrestrial. *Limulus* is marine. Many are nocturnal such as the Solifugae and Phalangids, and many, such as the spiders, weave webs and have specialized "silk" glands. In some cases, markedly in the Acarines, enormous numbers of individuals live together, but they show no adaptations to a communal life and no individuals, specialized to perform certain pieces of work, occur as they do occur among the social insects. Of the air-breathing Arachnids the earliest fossils

belong to the Scorpionidea and are found in the Silurian deposits ; spiders and Pedipalpi are also Palaeozoic but do not occur before the Carboniferous.

The following classification of Arachnida is adopted in this work :—

- Sub-class I. PANTOPODA (p. 781).
- Sub-class II. MEROSTOMATA (p. 785).
 - Order (i) Xiphosura (p. 786).
 - Order (ii) Eurypterida (Extinct, p. 796).
- Sub-class III. EUARACHNIDA
 - Order (i) Scorpionidea (p. 798).
 - Order (ii) Pedipalpi (p. 807).
 - Order (iii) Araneida. (p. 811).
 - Order (iv) Palpigradi (p. 827).
 - Order (v) Solifugae (p. 829).
 - Order (vi) Pseudoscorpionida (p. 833).
 - Order (vii) Podogona (p. 836).
 - Order (viii) Phalangidea (p. 837).
 - Order (ix) Acari (p. 842).

Sub-class I. PANTOPODA (PYCNOGONIDA).*

A peculiar group of Arachnids in which the segments corresponding with the meso- and meta-soma (abdomen) have disappeared. The eighth segment—that which corresponds with the pre-genital evanescent segment in Limulus and Scorpions—exists and bears fully developed legs on which the genital pore opens, though the latter may be repeated on the fifth and sixth and seventh segments.

The Pantopoda are all marine and are usually found crawling slowly over sea-weed or amongst zoophytes. The body is always small as compared with the legs, and it consists of four regions (Fig. 509). The first of these bears anteriorly the proboscis at the tip of which is the small, triangular mouth. The proboscis is regarded as an outgrowth of the parts surrounding the mouth and it varies greatly in form and size. It may be almost immovably connected with the prosoma or it may be articulated and so movable. Behind, four anterior, primitive somites are fused to form the

* Hoek, *Challenger Reports*, vol. iii, No. 2, 1881. Dohrn, *Fauna and Flora d. Golfes v. Neapel*, iii, 1881.

first region. This bears four pairs of appendages usually called (i) the mandibles, two- or three-jointed and often chelate; (ii) the palpi, three- to ten-jointed: either the mandibles or the palpi may be absent in the adult or at some embryonic stage, but they are always present sooner or later; (iii) the ovigerous

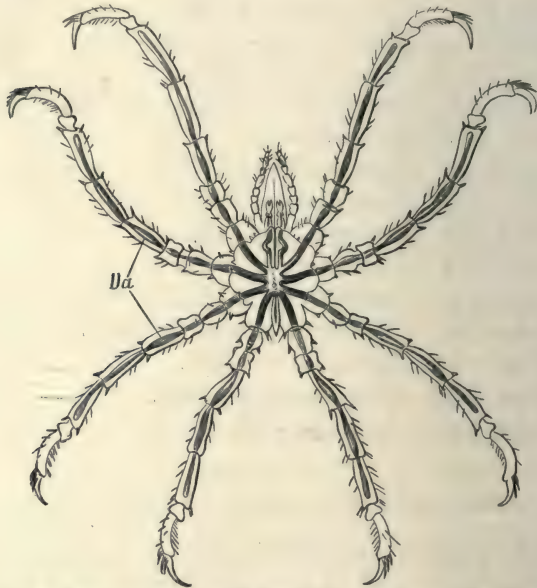


FIG. 508.—*Ammothea pycnogonoides* (règne animal). *Da* prolongations of alimentary canal into the legs.

legs, always present in both sexes; they are usually ten-jointed and in the male bear the eggs. The posterior part of the first region bears two lateral processes at whose extremities (iv) the first walking legs are articulated. The legs are eight-jointed and end in a claw and in some cases two accessory claws. Behind this first region come three free segments corresponding with the sixth and seventh and eighth somites of the scheme (p. 775), each bearing a pair of walking legs at the end of lateral processes which stick out from the body. Between the last pair of processes a tubercle projects which bears the anus at its end: this is the rudimentary abdomen.

Pantopods usually possess four eyes situated on a tubercle borne dorsally on the first region. Even when the eyes are absent,

which is often the case in deep-sea species, the tubercle persists.

The chitinous cuticle which covers the body is provided with numerous cavities which open to the exterior by narrow canals. There are no specialized respiratory organs and Hoek holds the view that these cavities assist in the necessary exchange of respiratory gases. The cuticle also bears bunches of bristles, probably sensory. It is lined by a nucleated, protoplasmic layer which represents the ectoderm. Numerous glands open to the surface, especially on the palps and on the ovigerous legs where their secretion serves to attach the eggs in the male during the breeding season.

The nervous system consists of a chain of four or five ganglia. The first or supra-oesophageal gives rise to the nerves which supply the mandibles or first pair of appendages and the eyes, and to an azygos dorsal nerve which runs to the proboscis and there forms a ganglion. The first sub-oesophageal ganglion sends off a pair of nerves to the proboscis, each of which also forms a ganglion, and the three ganglia in the proboscis are connected by a periproboscidial nerve ring. From the sub-oesophageal ganglion two more pairs of nerves arise, the anterior of the two run to the palps or second appendages and the other to the ovigerous legs. This ganglion consists in the young forms of two separate ganglia which subsequently fuse. The sub-oesophageal ganglion is followed by a chain of four or more (rarely of three) thoracic ganglia, which supply the four pair of legs and give off nerves posteriorly to the rudimentary abdomen.

The proboscis is traversed by an oesophagus lined with a chitinous lining which is produced into spines and teeth and plates. The latter are conspicuous in the enlargement which occurs in the oesophagus before it leaves the proboscis and, as numerous muscles run from them to the wall of the proboscis, it is not unlikely that they act as a suctorial apparatus. Behind the nerve-ring the oesophagus projects into the stomach so as to form a valve and in this region certain glands are described. The stomach is beset with glandular villi and it gives off a certain number of tubular digestive caeca which may extend into the proboscis and which do extend into the legs and mandibles even as far as the sixth joint. A short rectum leads to the anus which in *Colossendeis* is laterally placed.

There is a dorsal heart with usually three pair of ostia and

an anterior pore from which the blood flows when the heart contracts. In *Colossendeis* there is no pericardium. Respiration is cutaneous.

The testes are two longitudinal tubes lying in the body and connected posteriorly so as to be U-shaped. They give off segmentally arranged vasa deferentia which pass to open on the tibial or fourth joint of either all the walking legs, or of three pair, or of two. The ovaries are shaped primitively like the testis, but in many forms the portion in the body atrophies and the ova all arise from lateral portions which have grown into the legs. The fertilization is external and the males carry off the eggs on their ovigerous legs. The young are often hatched with only the three anterior appendages.

Dr. Hoek * divides the Pantopoda into four families :—

Fam. 1. **Nymphonidae.** In this family the mandibles and palpi are well developed, the ovigerous legs present in both sexes and as a rule they bear denticulated spines. The only genus is *Nymphon* with some forty species.

Fam. 2. **Colossendeidae.** Mandibles rudimentary or absent, well developed palpi, and ovigerous legs in both sexes as a rule with denticulate spines. This family is by far the largest in the number of genera it contains, *Ammonothea*, *Böhmia*, *Phanodemus*, *Rhynchothorax*, *Pepredo*, *Platycheilus*, *Oiceobathes*, *Ascorhynchus*, *Zetes*, *Parazetes*, *Pariboea*, *Alcinous*, *Achelia*, *Tanystylum*, *Lecithorhynchus*, *Oorhynchus*, *Colossendeis*, *Pasithoe*, *Endeis*, *Discoarachne*, *Barana*, *Clotenia*, *Trygaeus*.

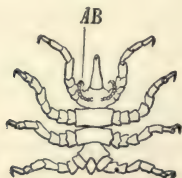


FIG. 509.—*Pycnogonum littorale*,
AB pair of legs used for carrying the eggs.

Fam. 3. **Pallenidae.** Strongly developed, chelate mandibles, palps rudimentary or absent. Only three genera; *Pallene* with ovigerous legs in both sexes furnished with denticulate scales; and *Phoxichilidium*, some species with ovigerous legs present in both sexes but without denticulate scales, in other species the ovigerous legs are confined to the males; *Neopallene*.

Fam. 4. **Phoxichilidae.** Mandibles and palpi absent or rudimentary. *Hannonia* has ovigerous legs in both sexes but no denticulate spines, *Phoxichilus* and *Pycnogonum* have them only in the male.

* We have followed Dr. Hoek in this scheme of classification, but in Lankester's article the Nymphonidae with the genus *Nymphon* and the Pallenidae with the genus *Pallene* are grouped together as the Nymphonomorpha. The family Ascorhynchidae with the genera *Ascorhynchus* and *Ammonothea*, together with the family Colossendeidae with the genera *Colossendeis* and *Discoarachne*, make up the group Ascorhynchomorpha; whilst a third group, the Pycnogonomorpha, comprise the family Hannoniidae with the genus *Hannonia* and the Pycnogonidae with the genera *Pycnogonum* and *Phoxichilus*.

Sub-class II. MEROSTOMATA.*

Aquatic Arachnida with a fused cephalothorax (prosoma), a more or less completely segmented abdomen, and broad abdominal appendages, in some and probably in all cases provided with foliaceous branchiae. The appendages of the pregenital segment appear to persist, though the segment itself is evanescent.

The name Merostomata (Dana) is here used as adopted by H. Woodward, and in place of Gigantostraca, which has been employed in antithesis to the crustacean divisions Entomostraca and Malacostraca. The subdivision Eurypterida is used in the sense adopted here by Huxley (Lectures on Natural History).

The Merostomata † are characterized by the modification of the coxal segments of the second to the sixth cephalothoracic limbs to subserve mastication. The first pair of apparent limbs (chelicerae) are chelate, and do not take part in limiting the mouth space. The last pair (seventh) are represented in the Xiphosura by a pair of unsegmented appendages (the chilaria), to which the more or less deeply divided median plate, the metastoma, apparently corresponds in the Eurypterida. The abdomen in the latter group is completely segmented into twelve segments, as in the Scorpions; of these the anterior six only are indicated in the recent Xiphosura, although intermediate conditions are presented by fossil forms. The anterior five or six segments of the abdomen bear broad plate-like limbs. In the Xiphosura the second to the sixth of these are furnished with foliaceous branchiae, and there are indications of similar structures in the

* Woodward, "Monograph of the Brit. fossil Crustacea belonging to the order of Merostomata." P. I., & II., *Palæont. Soc. of London*, 1866-1869. Woodward, "On some points in the structure of the Xiphosura, having reference to their relationship with the Eurypteridae," *Quarterly Journ. Geol. Soc. of London*, 1867 and 1871. Dohrn A. Zur Embryologie u. Morphologie von *Limulus polyphemus* *Jen. Zeits.*, vi, 1871. Milne Edwards, A., Recherches sur l'anat. des Limules, *Annales d. Sciences Nat.*, Sér. v, T. xvii, 1873. Packard, A. S., The anatomy, histology and embryology of *Limulus polyphemus*. *Mem. Boston Soc. Nat. Hist.*, Boston, 1880. Lankester, E. R., *Limulus* an Arachnid, *Quart. Journ. Mic. Sc.*, xxi, 1881. Schmidt, Fr., Crustaceen fauna der Eurypteren schichten von Rootziküll auf Oesel *Miscell. silurica*, iii, *Mém. Acad. Imp. de St. Pétersbourg*, Sér. 7, T. xxxi, No. 5, 1883. Kingsley, J. S., The embryology of *Limulus*, *Journ. Morph.*, vii and viii, 1892-3. Kishinouye, On the development of *Limulus longispina*, *Journ. Coll. Sc.*, Japan, 1882. Patten, W. and Redenbaugh, W. A., Studies on *Limulus*, *Journ. Morph.*, xvi, 1890. Holm, G., Ueber die Organisation der *Eurypterus fischeri*, *Mém. Acad. Imp. d. Sc. de St. Pétersbourg*, Sér. 8, Cl. Phys. Math., vol. viii, No. 2 (1897).

† *μνρός* a thigh.

Eurypterida. A spine-like or plate-like telson terminates the body.

The Xiphosura consists of the recent species of King Crabs, with some allied fossil forms, but no remains of the Eurypterida have been found subsequent to the Carboniferous period.

Order 1. XIPHOSURA.

Merostomata with the abdomen consisting, in the recent members,

of six fused segments anteriorly, bearing six biramous appendages, and of an unsegmented posterior region. The seventh cephalothoracic appendages (chilaria) are distinct and unsegmented.

The body of *Limulus*, the King Crab or Horseshoe Crab, is divided into three parts which may be called, without implying an exact homology with parts so named in other groups, the cephalothorax, abdomen and caudal spine. It is covered with a firm smooth

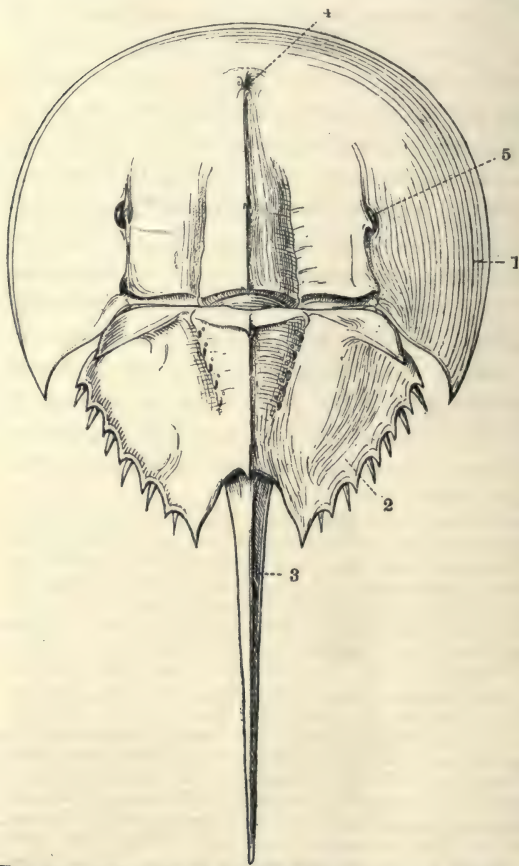


FIG. 510.—Dorsal view of *Limulus polyphemus* $\times \frac{1}{2}$. 1 cephalothorax; 2 abdomen; 3 caudal spine; 4 median eyes; 5 lateral eyes (from Shipley and MacBride).

cuticle bearing the appearance of lacquer, and parts of the under surface are clothed with hairs.

The cephalothorax is semicircular in outline, with projecting postero-lateral angles. It is convex above and presents three longitudinal spinose ridges, a median and two lateral. A pair of **median eyes** are situated one on either side of the anterior spine of the median ridge, and two large **lateral eyes**, considerably further back (at the level of the mouth) and external to the lateral ridges. On either side of the median ridge is a longitudinal groove, both of which, like the ridge between them, are continued back on the abdomen and give rise to a tripartite division of the body recalling that of Trilobites, a resemblance which the fuller knowledge of the structure of these animals which we now possess shows to be only superficial. The mouth is situated far back and the under surface of the cephalothorax is deeply excavated to allow play to the limbs which are grouped about it.

The **abdomen** is movably articulated with the cephalothorax, and deeply notched behind for the caudal spine. Its lateral margins, which converge posteriorly, bear 6 movable spines inserted into notches. Corresponding to these spines, and to the limbs borne on the ventral surface, 6 paired depressions are found in the longitudinal grooves on the dorsal surface, indications of a segmentation of the anterior part of the abdomen which is much more obvious in the embryo. Like the cephalothorax the abdomen is deeply excavated below for the reception of appendages. The caudal spine is movably articulated with the abdomen and the anus opens ventrally at its base.

A comparison with the Eurypterids and with *Scorpio* shows that the region of the abdomen behind the last (6th) abdominal limbs represents the six posterior segments of the bodies of these animals. The three anterior (7th-9th) of these are for a brief period defined in *Limulus*, by the segmentation of the larva.

A prominent longitudinal ridge, laterally flattened, the *camerostome*, lies in front of the mouth, in a portion corresponding with the upper lip of Crustacea and the labrum of insects. Behind the mouth is an oval cushion-like area, covered with short hairs, the *promesosternite* of Lankester. The **appendages** of the cephalothorax are grouped in a ring about the mouth and this area. They are seven in number. The most anterior, the *chelicerae* (I), are slender and chelate, consisting of three

segments, and are inserted by narrow bases at the antero-lateral angles of the camerostome. The five succeeding pairs

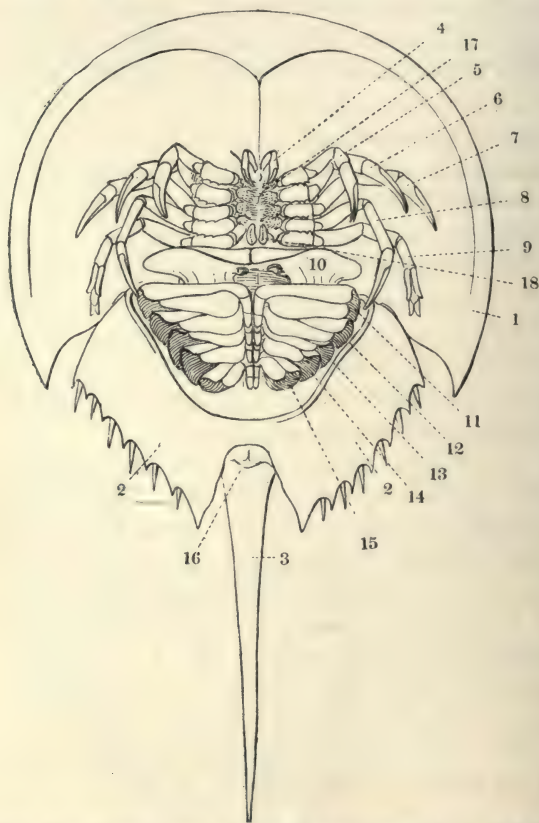


FIG. 511.—Ventral view of *Limulus polyphemus* $\times \frac{1}{2}$. 1 cephalo-thorax; 2 abdomen; 3 caudal spine; 4 chelicerae; 5-9 the five legs; 10 genital operculum (1st abdominal appendage); 11-15 branchiate appendages (abdominal appendages 2-5); 16 anus; 17 points to the region of the mouth; 18 chilaria (7th cephalo-thoracic appendages) (after Shipley and MacBride).

subserve the double function of mastication and locomotion. Their broad bases of insertion are produced internally into spinose masticatory lobes, which form the lateral boundaries of the extra-oral space. In the female the four anterior locomotory limbs (II-V) are chelate, while in the adult male (the young males resemble the females) the first (II), (in *L. moluccanus* and *L. longispina* the first two—

II and III) end in curved claws. The fifth pair (VI) differs from the others by the possession of a peculiar curved spathulate process articulated to the outer aspect of its base, by its non-chelate termination, and by the presence of a group of four broad imbricated spines, which are separately movable, at the distal end of the antepenultimate segment. These are used in shovelling back the mud or sand in which the animals live, and in propelling them forward. The spathulate process recalls a crustacean

exopodite and helps to separate and hold apart the gill-book appendages.

The seventh pair of appendages are the *chilaria* of Owen (VII). They are unjointed flattened processes, projecting vertically downwards, and limiting the extra-oral space posteriorly.

The significance of these processes has been much debated, and their appendicular nature denied, but Kishinouye's discovery of a mesoblastic somite and a pair of ganglia in the ventral chain corresponding to them in the embryo, and Brauer's demonstration of a transient pair of appendages in their position in the embryo of the Scorpion, remove all doubt as to their nature.

The number of the abdominal appendages is six pairs, corresponding to that of the depressions in the upper surface and of the movable spines at the sides. They are lamellar in form and resemble the limbs of many Crustacea in so far as they are partially divided into a slender internal process and a broad external plate. The appendages of the anterior pair (Fig. 511, 10) are united in the middle line for the greater part of their length to form the *operculum* (VIII) which bears the paired generative apertures near the base on the posterior aspect. The opercular endopodites are more prominent in the female than in the male. The operculum is inserted, in the adult on the hinder part of the cephalothorax, but in the embryo its halves are clearly seen to be the appendages of the anterior abdominal segment.

In the remaining five pairs (IX–XIII) the appendages of opposite sides are free from one another (the sterna of the segments from which they spring being each produced into a pointed process between them) and their exopodites bear on their posterior surfaces the delicate branchial lamellae, superposed like the leaves of a book, to the number of 150 to 200 for each limb (Fig. 512). The animal is able to propel itself in the water by the flapping action of the abdominal appendages.

A remarkable skeletal structure, the *entosternite*, lies in the

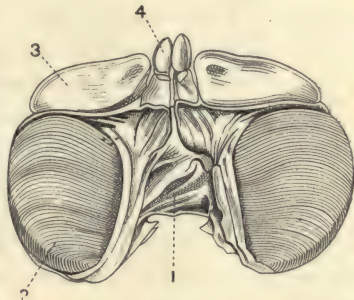


FIG. 512.—Posterior aspect of one of the branchiate abdominal limbs of *Limulus*. 1 sternite of the segment; 2 branchial lamellae; 3 outer, and 4 inner plate of the appendage (after Van der Heyden).

interior of the cephalothorax dorsal to the ganglionic chain and ventral to the alimentary canal. It is a bilaterally symmetrical cartilaginous plate, unconnected with the exoskeleton, and serves as the point of origin of muscles. A similar structure is found in Scorpions and Spiders (p. 778), and also among the Crustacea (*Apus*, etc.).

The **Central Nervous System** of the adult is highly concentrated. The brain, which forms a compact mass obscurely divided into lateral halves, together with the succeeding ganglia as far as that of the first abdominal (opercular) segment, form an oval ring round the oesophagus, from which a double cord extends into the abdomen, with ganglia and nerves corresponding to the posterior abdominal appendages.

Its composition has been elucidated by Kishinouye, Patten and others. It appears that the brain is composed of two pairs of ganglia, an anterior and posterior, united by commissures, of the large ganglia of the lateral eyes, and of a median ganglion supplying the median eyes. Its under surface becomes markedly convoluted in the adult. Besides the eyes it supplies the median olfactory area. The ganglia of the *chelicerae* (the first postoral) do not fuse with the brain as they do in the Scorpion.

In the embryo a pair of ganglia on the double ventral cord corresponds to each pair of thoracic (including the *chilaria*) and abdominal appendages, and a terminal pair, behind those of the 6th abdominal, supply the hinder part of the body.

Sense Organs. Sensory cells are abundant on the masticatory processes of the thoracic limbs and on their chelae, and over a slightly elevated median area, the **olfactory organ**, lying in front of the camerostome (Patten).

The **median eyes** lie close together on either side of a median spine. Like the median eyes of the Arachnida generally they consist of two well-marked layers of cells—an upper, forming the “vitreous body” continuous with, and little modified from, the adjacent cells of the hypodermis, and a deeper layer forming the *retina*. Both layers are concave, in adaptation to a lenticular thickening of the cuticle. The cells of the retina are large and oval, and prolonged into nerve fibres. They are arranged in groups (ommatidia) each consisting of some 7 cells enclosing a rhabdome between them, and are surrounded by dark pigment. It is possible that the median eyes of *Limulus* are partially degenerated structures.

The **lateral eyes** (Fig. 513) consist of a single layer of hypodermic cells in contact with the transparent cuticle, which is produced

downwards into numbers of conical processes, each forming a lens. Beneath the processes the hypodermal cells are arranged in globular *ommatidia*, which resemble taste-bulbs. They consist of cells (*retinulae*), each with a highly refracting inner border (rhabdom), grouped in varying numbers, commonly from 9 to 11, about a central ganglion cell. The retinulae and the ganglion cell are produced into nerve processes, which unite in a plexus below the hypodermis, and the former, as well as the hypodermic cells about them are highly pigmented. Between the ommatidia the hypodermic cells retain their simple columnar character (Watase).

The lateral eyes present a very simple form of compound eye, the elements of which are largely distinct. In the other Arachnids the lateral eyes of *Limulus* are represented by groups of eyes (Lankester and Bourne). In these the ommatidia are much reduced in subordination to the function of the eye as a whole.

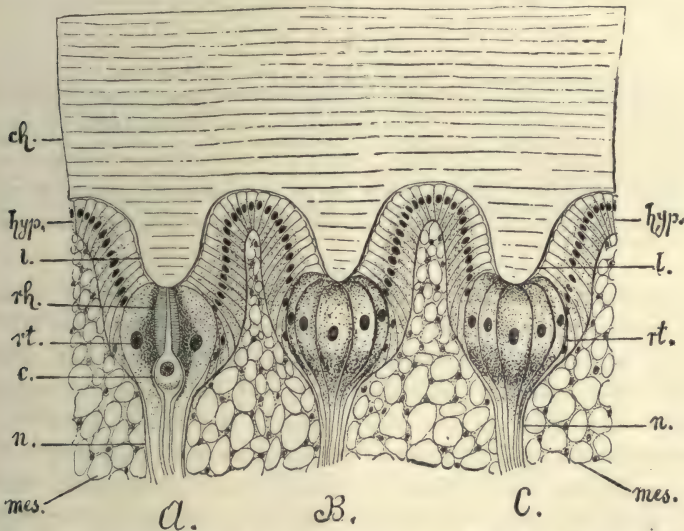


FIG. 513.—Three ommatidia of the lateral eye of *Limulus*. B and C show the ommatidia in surface view, A in longitudinal section. c Central ganglion cell; ch chitinous cuticle; hyp hypodermis; l lenticular cone; mes mesodermal tissue; n nerve; rh rhabdom; rt retinula (from Korschelt and Heider after Watase).

Both median and lateral eyes arise on the cephalic lobes of the embryo (Kishinouye), though they soon shift to a more posterior position. The **median eyes** arise, as in Scorpions and Spiders (p. 336), from an invagination of the epiblast immediately in front of the thickening for the brain. The invaginated cells grow forward as a cord (single or double ?) whose end

abuts against the epiblast cells of the surface at a point a little anterior (dorsal) to the point of invagination. Here the median eyes are formed. The mode of their development has not been followed in detail, but it appears to be similar to that of the median eyes of *Scorpio*. The cells of the superficial epiblast (hypodermis) secrete the lens, and become the "vitreous body." The underlying cells of the invagination, the originally deep ends of which are now directed towards the surface, form the retina.

In the case of the lateral eyes no invagination leading to a reversal of the retinal layer occurs.

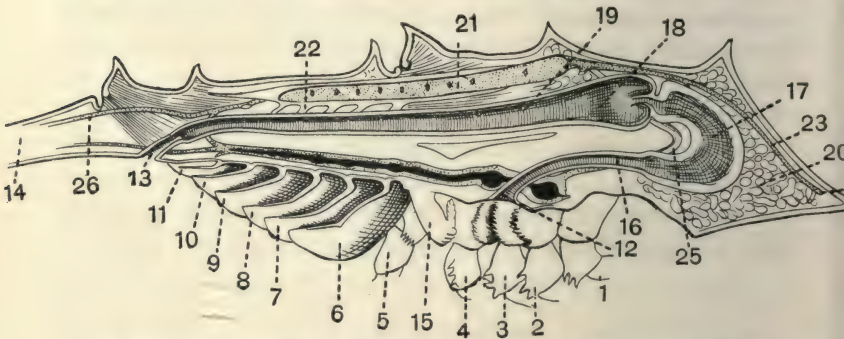


FIG. 514.—*Limulus polyphemus*. Diagrammatic view of the left half of the body, seen from the inner side. 1–5 the second to the sixth cephalothoracic limbs (the first, left chelicera, is hidden by the camerostome, above the base of 1; the seventh, the left chilidium, is numbered 15); 6 the operculum; 7–11 the second to the sixth abdominal limbs; 12 mouth; 13 anus; 14 caudal spine; 15 chilidium; 16 oesophagus; 17 proventriculus; 18 intestine; 19 the openings of two hepatic ducts; 20 lobes of the liver; 21 heart with eight venous ostia; 22 branchial veins, returning the blood to the pericardium; 23 anterior median (frontal) artery; 24 its point of division into two marginal arteries; 25 anterior paired artery; 26 supra-anal artery; the subanal is seen below it. The central nervous system is represented in black, surrounded by a blood sinus (from Shipley and MacBride, after Leuckart, and, in part, after Packard).

Alimentary Canal. From the mouth the oesophagus passes forwards and dilates first into a proventriculus and then into a somewhat globular muscular stomach, whose walls are raised into ridges and covered with chitin. At the projecting pyloric orifice (the limit of the stomodaeum) the chitin ends. The **intestine** runs straight back to the short rectum, receiving in the cephalothorax the orifices of the two pairs of hepatic ducts. The **Liver** is of great size, and disposed in symmetrically arranged masses, its acini together with those of the generative gland forming a packing for the other organs of the cephalothorax. It also extends back along the intestine into the abdomen.

The **Heart** (Fig. 515) is fusiform, and lies dorsal to the intestine over its anterior three quarters. It is surrounded by a pericardial sinus, communicating with it by eight pairs of **ostia**. It gives off an anterior median (frontal) and five paired arteries,

of which the anterior pair (named aortic arches), arching over the intestine, supply a continuous investment of sinuses to the whole of the central nervous system, and some of its branches. There is a very complete system of arteries and veins, and the blood on its return journey to the heart enters two great longitudinal trunks (11), from which it flows to the six abdominal appendages, in the five posterior of which it is aerated. From these it is returned to the pericardial sinus (A. Milne-Edwards).

The blood is of an indigo blue colour owing to the presence of haemocyanin. It contains granular amoeboid corpuscles.

The **Excretory organs**, long known as the "brick-red glands," consist of four lobed masses, lying ventrally in the cephalothorax, opposite appendages II-V, and of a longitudinal tract uniting them. From the posterior part of this a convoluted duct leads, according to Patten, to a papilla at the base of the fifth pair of legs. Until the discovery of this papilla by Tower, the duct was supposed to be closed in the adult. Internally the duct communicates by a funnel-shaped opening with a cavity in the posterior lobe of the gland, the remains of the coelom of the fifth thoracic segment. In the embryo, lobes are also situated in the first and sixth segments.

The **Reproductive organs** have a similar disposition in the two sexes. The testes and ovaries consist of systems of ramifying

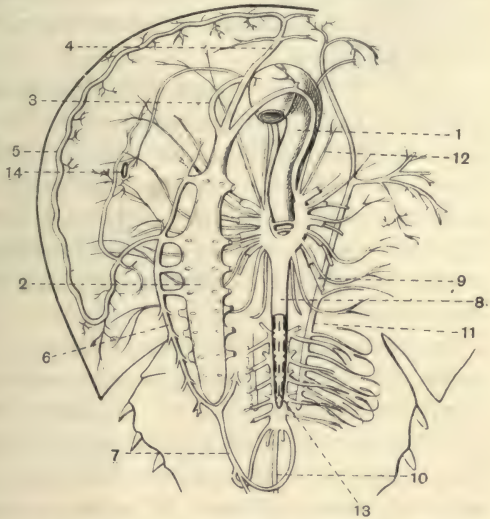


FIG. 515.—Diagram of the circulatory system of *Limulus*. 1 Oesophagus; 2 heart with eight pairs of ostia; 3 "aortic arches"; 4 frontal artery; 5 marginal artery; 6 collateral artery, receiving four (paired) vessels from the heart; 7 supra-anal artery; 8 arterial sinus investing the ventral nerve cord; 9 nerve to one of the legs, at its base the arterial trunk investing the nerve is indicated; 10 sub-anal artery; 11 longitudinal trunk giving off vessels to the abdominal appendages; 12 a nerve without a vascular sheath; 13 ventral nerve cord contained in arterial sheath; 14 lateral eye (modified from Leuckart, after Milne Edwards).

tubes lying in the cephalo-thorax and the abdomen. In each there is a median abdominal portion lying dorsal to the intestine and an anterior portion forming a widely distributed network of tubes packed among the acini of the liver. From these the paired efferent ducts pass downwards to open by slightly projecting orifices on the posterior aspect of the operculum. The relation of the ducts with the coelomic spaces of the embryo has not been followed.

The males are smaller than the females and are further distinguished by the hooked, not chelate, termination of the second, or second and third appendages, a character which they acquire on arriving at maturity. The spermatozoa have an oval head and a flagellum.

At the breeding season the animals (*L. polyphemus*) come ashore in pairs, at high spring tides, the male clinging to the carapace of the female. The eggs are fertilized after they have been deposited in the series of hole which the female digs for their reception. The point selected is near the upper limit of high tide, and the mass of eggs produced is said to be about half a pint in volume. *L. longispinus* of Japan appears to have similar habits.

In development a blastodermic area is formed on the ventral surface of the yolk. A depression representing the blastopore forms and lengthens into a "primitive groove," at the anterior and posterior ends of which the mouth and anus are formed. The mesoderm is formed by proliferation of the cells along the primitive groove. Later it becomes segmented and coelomic cavities appear by splitting of the mesoblast, in some of the segments. The relation between the fifth pair and the excretory organs is noticed above, and also the existence of a pair of mesoblastic somites and of a pair of ganglia corresponding with the *chilaria*, thus establishing their character as appendages.

On escaping from the embryonic cuticle the young *Limulus* is without an elongated caudal spine and swims freely by means of its abdominal appendages, of which only three pairs have as yet been formed (Fig. 516). With its marked lateral eyes, segmented abdomen and body divided into median and lateral regions by longitudinal grooves, it presents considerable resemblance to a Trilobite, and the stage has in fact been called the *Trilobite stage*. The number of segments composing the anterior division of the

body, and the nature of the appendages, however, render it highly improbable that the resemblance, striking as it at first appears, has any phylogenetic significance.

After the first moult the caudal spine begins to elongate, and at this stage, while the abdomen retains its segmented larval character, a true affinity with the fossils *Prestwichia* and *Belinurus* of the palaeozoic rocks is clearly revealed.

Four living species of King Crab are known*: *L. polyphemus* from the eastern coast of the United States, *L. longispinus* from China and Japan, and *L. moluccanus* and *rotundicauda* from the East Indies. They frequent muddy shores where the water is two to six fathoms in depth, and often bury themselves in the mud. Their food consists of annelids, such as *Nereis*, and bivalves.

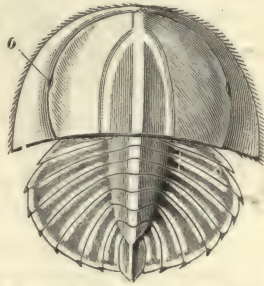


FIG. 516.—Embryo of *Limulus*, in the so-called "Trilobite stage." o Lateral eye (from Claus after Dohrn).

Fossil species of *Limulus* occur in Jurassic and Triassic rocks; while in the palaeozoic times an allied family, the *Hemiaspidae*, existed whose members (*Hemiaspis*, *Belinurus*, *Prestwichia*) resembled the young *Limulus* after its first moult. They may hence be regarded as persistent larval forms. The abdomen was much more completely segmented than that of *Limulus*, and in *Hemiaspis* there is a division into pre- and post-abdomen, affording a transition to the Eurypterida and the Scorpions.

On comparing *Limulus* with the Crustacea, with which it has, until recently, been usually classified, we notice as conspicuous points of difference the absence of appendages corresponding with the first antennae, the division of the body into parts, of which the anterior includes seven segments,† and the absence of a stage of development corresponding to the nauplius larva. The most definitely Crustacean feature is the biramous character of the abdominal appendages; and the existence of median and compound lateral eyes makes, though less strongly, in the

* See, however, Pocock, *Ann. Mag. N.H.* (7), 9, 1902, p. 256.

† The development of the camerostome from paired rudiments raises the question whether it is not the representative of a pair of appendages anterior to the chelicerae (p. 323).

same direction. The Eurypterida, though more primitive than *Limulus* in the complete segmentation of the body, afford no support to its Crustacean affinities; on the contrary they present a highly specialized feature in the fusion of the seventh pair of limbs to form the metastoma.

On turning to the air-breathing *Arachnida* we find, as was partially recognized long ago by Straus Durkheim, an almost complete correspondence in the adult structure, and the investigation of the development of *Limulus* and of *Scorpio* has brought to light further resemblance, and also cleared up points of apparent differences.

It appears that we have in *Limulus* a member of the Arachnida, which retains the primitive water-breathing habit, and, in the features of the abdominal appendages, some traces of the characteristic structure of the far off crustacean stock from which the Arachnida originally sprang.

Order 2. EURYPTERIDA.

Merostomata with the abdomen completely divided into twelve segments, of which the five anterior bear appendages. A metastoma is present, apparently representing the seventh cephalothoracic limbs.

The Eurypterida were aquatic (marine and freshwater) forms, preserved in the Palaeozoic rocks from the Silurian to the Carboniferous. In some respects they are intermediate between *Limulus* (Xiphosura) and the Scorpions, notably in the complete segmentation of the abdomen, and the more anterior position of the mouth. The mouth cavity (i.e. the cavity lying outside the mouth proper and between the bases of the second to the sixth appendages) is closed behind and below by a large oval plate, the metastoma, presenting a deeper or shallower notch in the anterior border. It corresponds in position with the chilaria of *Limulus*, and apparently represents these appendages fused together. If this conclusion is correct the cephalothoracic appendages correspond in number with those of *Limulus*. The chelicerae* are chelate, and are short and included between the second pair of appendages in *Eurypterus*, or long as in *Pterygotus*.

* The presence of these appendages in *Eurypterus*, suspected by Laurie,

The sixth pair of limbs are large and paddle-like. The five anterior abdominal segments bear plate-like appendages, overlapping one another from before backwards, and are so arranged

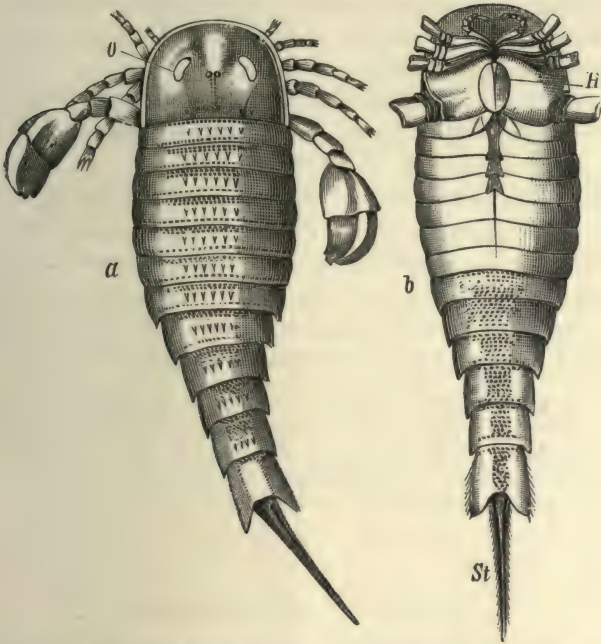


FIG. 517.—*Eurypterus remipes* after Nieszkowski. *a* Dorsal view; *b* ventral view; *H* metastoma; *O* eyes; *St*. caudal spine.
N.B.—In *b* the chelicerae are omitted and one segment too many is represented in the anterior abdominal region.

lapping one another from before backwards, and are so arranged that the exposed part of the fifth lies beneath the sixth tergal plate. The first, known as the operculum, is traversed by a transverse suture, so that it has the appearance of representing two pairs of appendages. The appendages were separated from one another by a suture in the middle line, and oval patches on the upper surfaces of the four posterior pairs are apparently the remains of foliaceous branchiae.

One set of individuals, larger than the others, and regarded by Holm as females, bear a prominent complex median organ has been demonstrated by Schmidt and by Holm in the material from the island of Oesel in the Baltic. The fossils are here contained in calcareous beds of the Silurian, and by dissolving the matrix with acid these authors have succeeded in obtaining the chitinous elements free. When mounted in canada balsam, the preparations show the details of structure in great perfection.

projecting backwards between the halves of the operculum, and covering paired styles which project in the corresponding position from the second pair of appendages. Only a small shield-like median structure is found between the halves of the operculum in the supposed males.

The six posterior abdominal segments are closed rings and the anus opened on the last. The telson is spine-like in *Eurypterus*, a flattened plate in *Pterygotus*.

In addition to the sexual differences above noted (in size, and the structure of the organs on the first and second abdominal segments), the supposed males have, in *Eurypterus*, a hook-like (clasping ?) structure on the third pair of cephalothoracic appendages, those which in the males of *Limulus* are also modified.

Some of the Eurypterida attained a length of nearly five feet.

Fam. 1. **Eurypteridae.** *Eurypterus* Dekay, some 20 spp. from Silurian to Carboniferous; *Stylonurus* Page, Silurian and Devonian; *Dolichopterus* Hall, with deeply cleft metastoma, Silurian N. Am.; *Slimonia* Page, Devonian of Scotland. *Pterygotus* Agassiz, with long powerful chelicerae, Ordovician and Devonian of Europe and N. America.

Sub-class 3. EUARACHNIDA

Air-breathing Arachnida with fused head and thorax (prosoma), with two pairs of jaws, four pairs of ambulatory legs, and apodal abdomen (meso- and meta-soma).

In this group the respiratory lamellae and the abdominal limbs bearing them have apparently sunk into pits in the body and given rise to the pulmonary sacs with their contained lung-books. In some forms the lung-books are replaced by tracheae.

Order 1. SCORPIONIDEA *

Arachnids with pro-, meso- and meta-soma clearly distinct; the prosoma is covered by a single dorsal tergum which bears median and lateral eyes; the small chelicerae and the large pedipalps are chelate; the 3rd, 4th, 5th, and 6th jointed appendages are walking

* Lankester, *Quart. J. Micr. Sci.*, xxiv, 1884; *Trans. Zool. Soc.*, London, xi, 1883. Lankester and Bourne, *Quart. J. Micr. Sci.*, xxiii, 1883. Brauer, *Zeitschr. wiss. Zool.*, lix, 1895. Lankester, *Quart. J. Micr. Sci.*, xxiv, 1884. Laurie, *Quart. J. Micr. Sci.*, xxxi, 1890 and xxxii, 1891. Pocock *An. Mag. Nat. Hist.* (6), xii, 1893. Kraepelin, *Scorpiones, Das Tierreich.* L. 8.

legs, the first two with gnathobases ; the first mesosomatic segment bears the genital operculum, and the second the pectines, the next four two lung-books ; the five posterior segments are

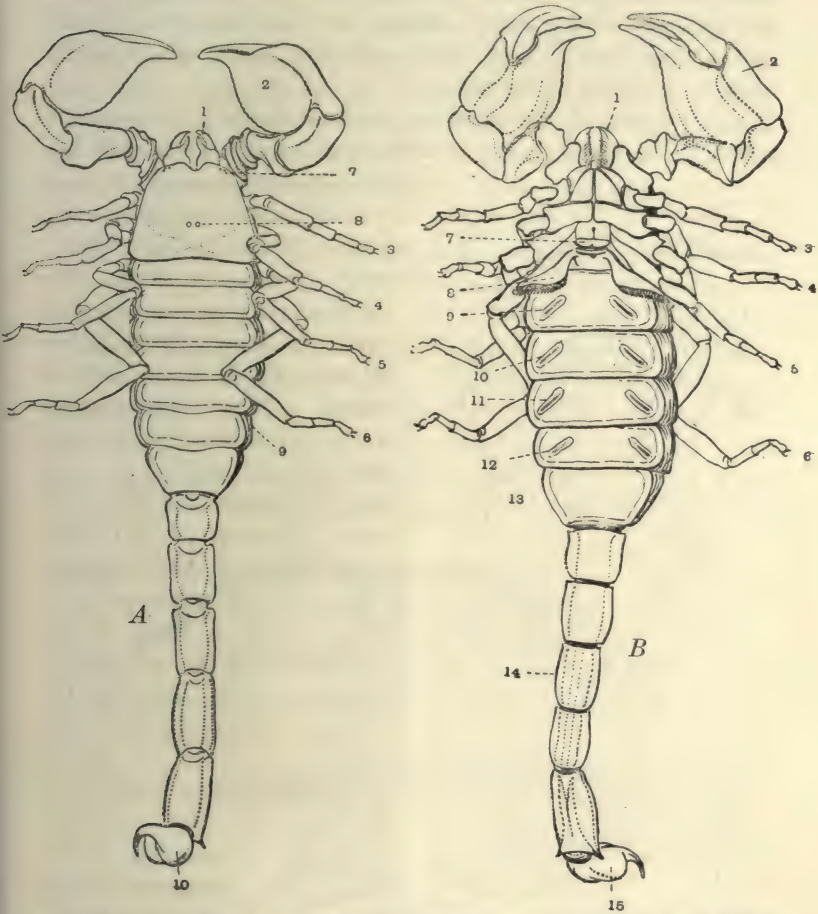


FIG. 518.—*A* Dorsal view of an Indian scorpion, *Scorpio swammerdami* $\times \frac{1}{2}$. *B* Ventral view of the same $\times \frac{1}{2}$. *A* 1 Chelicera ; 2 pedipalp ; 3, 4, 5, 6 3rd to 6th appendages, or walking legs ; 7 lateral eyes ; 8 median eyes ; 9 soft tissue at side of body, pleura ; 10 the poison sting or telson. *B* 1-6 as in *A* ; 7 the genital operculum ; 8 the pectines ; 9, 10, 11, 12 the four right stigmata leading to the four lung-books ; 13 the last segment of the mesosoma ; 14 the third segment of metasoma ; 15 the telson. In each case the metasoma, which is usually carried bent forward over the meso- and pro-soma, has been straightened out.

compressed and form a tail which ends in a post-anal sting provided with poison glands.

Scorpions are amongst the oldest of living animals of

which we have fossil record, having persisted with comparatively little change from Silurian times. They inhabit tropical and the warmer temperate countries, e.g. the Mediterranean area, but they are intolerant of the sun and usually lurk in crevices and under stones during the day-time but become active after dusk. Then they seek their food, which mainly consists of insects and spiders.

The tergum of the prosoma (cephalo-thorax) is somewhat square with often a low median keel. Near the middle line

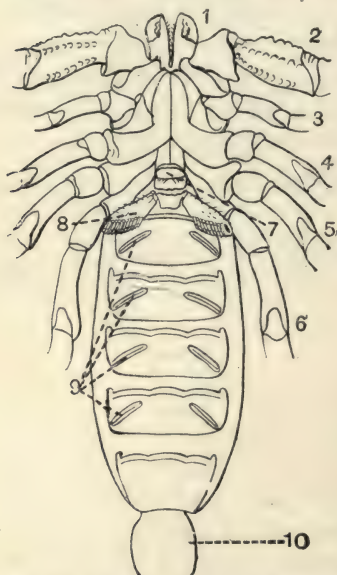


FIG. 519.—Ventral view of pro- and mesosoma of *Buthus afer* (from Leuckart, after Cuvier). 1 Chelicerae; 2 pedipalpi; 3-6 1st to 4th pair of ambulatory legs; 7 genital operculum; 8. pectines; 9 4 pairs of stigmata on the 3rd-6th mesosomatic region; 10 1st metasomatic segment.

are two central separate small eyes and at the edge are two to five lateral eyes (p. 334 ff). Some species are blind. The mesosomatic (pre-abdominal) terga are wide plates separated by soft skin from the ventral sterna. The metasomatic segments (post-abdominal) are encased in chitinous rings; they are compressed and show no trace whatever of soft skin except between each segment. The post-anal poison-sting is bulbous with a sharp point; close to the tip are two minute openings which communicate with two poison-glands in the bulb.

The appendages are as follows (Fig. 518):—

A. On the prosoma :

(i) The chelicerae, small three-jointed, chelate appendages almost hidden under the anterior edge of the prosomatic tergal shield; the teeth on the claws are of much systematic importance. (ii) The pedipalpi; these are the well-known six-jointed nippers of the scorpion with powerful chelate terminal claws, their coxae are produced in towards the mouth as a gnathobase. (iii), (iv), (v), and (vi) The walking legs; they are six-jointed, though a marking in the fourth joint may indicate a seventh; numbers

(iii) and (iv) have distinct gnathobases produced in towards the mouth (Fig. 519); each walking leg has two terminal claws; between the bases of (v) and (vi) is a plate of varying outline, the sternum or metasternite, whose shape is of great systematic importance. A segment belonging to the prosoma exists in the young embryo (p. 775), but it disappears at an early stage and leaves no appendages or indeed any other evidence in the adult that it ever existed; a similar segment also disappears in *Limulus* (p. 789); we have followed Lankester in omitting it from the enumeration of the adult segments.

B. On the mesosoma:

(vii) The genital operculum (Fig. 519), a foliaceous flap with traces of a paired origin, which, when lifted up, reveals the openings of the genital ducts. (viii) The pectines, each with a base bearing numerous processes like a comb; the function of these appendages is tactile. The appendages of segments (ix), (x), (xi) and (xii) consist of a base bearing some 140 flattened leaves which act as respiratory organs; in the adult they are contained in the pulmonary sacs, but in the embryo they arise as external processes which later sink into a pit pre-

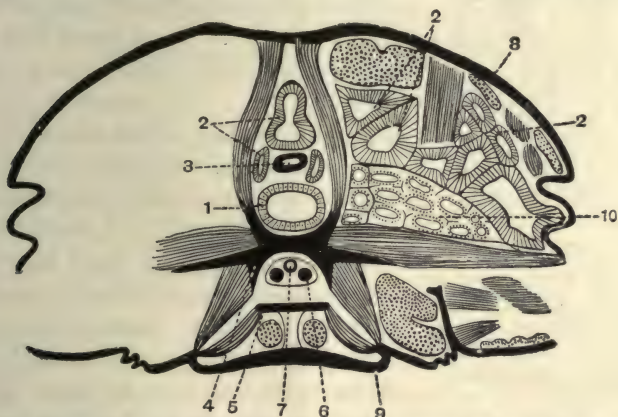


FIG. 520.—Transverse section through the body of *Euscorpium italicus* in the region of the endosternite and near the pectines (after Lankester). 1 Alimentary canal; 2 caeca of gastric gland (liver); 3 anterior aorta; 4 endosternite; 5 supraneural plate of endosternite; 6 right ventral nerve cord; 7 supraneural blood-vessel; 8 chitinous tergum; 9 chitinous sternum; 10 right coxal gland. The dotted areas represent sections of various muscles.

pared just behind them; had they remained outside the body they would have looked exactly as the gills of *Limulus* look (Fig. 512).

C. On the metasoma there are no appendages.

Within the body there is an internal skeleton in the form of the endosternite just as there is in *Limulus* and *Mygale*. It takes the form of a complex, triangular plate pierced with holes for the nerve-cord and for blood-vessels to traverse, and its edges are produced into processes for the attachment of muscles. Its texture is cartilaginous, though histologically and chemically it differs from vertebrate cartilage. It yields chitin instead of gelatine. It lies obliquely in the body and roughly divides the cavity of the prosoma from that of the mesosoma. Little is

known about its origin or about its function. There is a second small endosternite ventral to the nerve-cord in the segment which bears the pectines.

The mouth is minute as befits a creature which takes only liquid food, chiefly the blood of spiders or insects. It opens into a suctorial pharynx with elastic, chitinous walls. These walls can be divaricated by certain extrinsic muscles and thus the pharynx acts as a suctorial stomach. From this an oesophagus (Fig. 521) passes backward and receives the paired ducts of two salivary glands. Salivary glands are usually associated with terrestrial life and are not found in *Limulus*. The straight intestine, into which the oesophagus opens, runs without twist or curve to the anus. During its course it receives as many as five or six lateral ducts which lead from as many lateral gastric glands, often collectively termed

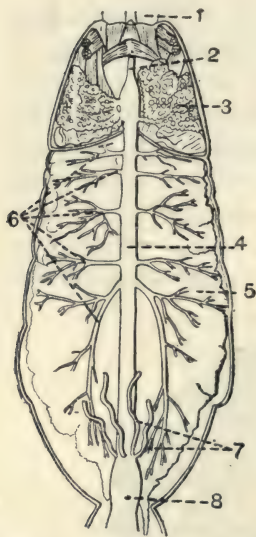


FIG. 521.—Dorsal view of *Buthus occitanus*, the dorsal integument has been removed to show the digestive organs (from Leuckart, after Blanchard). 1 Chelicerae; 2 oesophagus; 3 salivary glands; 4 intestine; 5 liver; 6 ducts of liver; 7 malpighian tubules; 8 intestine.

the liver. The food passes from the narrow intestine into the lumen of these glands and is there digested. At the anterior end of the metasoma the intestine receives the openings of two or four malpighian tubules engaged in excreting waste nitrogenous matter. The occurrence of these organs again seems to be favoured by a terrestrial mode of living and they have probably

arisen more than once in the history of invertebrates. In the scorpion they are said to originate from the mesenteron and are therefore lined by hypoblast, whilst in insects and most arachnids they grow out from the proctodaeum and so are epiblastic in origin.

There are however in scorpions and other Arachnids other glands engaged in the same work of ridding the system of nitrogenous excreta. These are the coxal glands. They lie one on each side in the prosoma just above the bases of the 5th and 6th appendages, and they open to the exterior in the young by a minute pore on the posterior face of the coxa of the 5th appen-

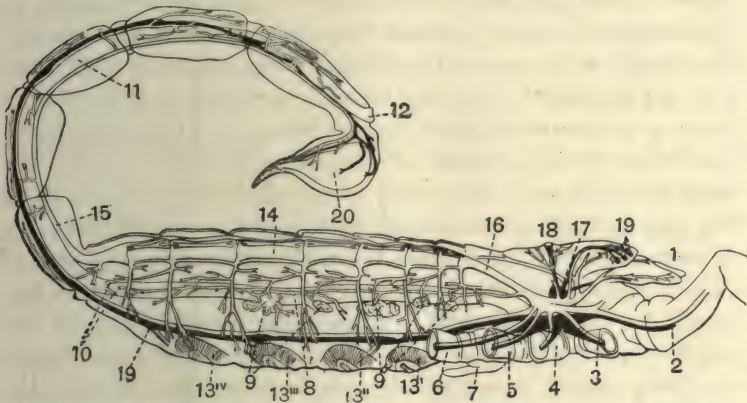


FIG. 522.—View of internal anatomy of *Butkus*, showing digestive, circulatory, respiratory, and nervous systems (from Leuckart, after Newport and Blanchard). 1 Chelicerae; 2 pedipalpi; 3-6 ambulatory limbs; 7 pectines; 8 mesenteron; 9 lobules of liver, with ducts entering mesenteron; 10 malpighian tubules, portions of; 11 proctodaeum; 12 anus; 13ⁱ-13^{iv} lung sacs; 14 heart; 15 posterior aorta; 16 anterior aorta; 17 brain; 18 median eyes; 19 (above) lateral eyes; 19 (below) nerve cord; 20 poison gland.

dage (3rd leg). At their inner end they open into a vesicle. The coxal glands are homologous with the green gland of Malacostraca and the shell glands of the Entomostraca and are derived from the coelom (see p. 317).

The blood of scorpions contains haemocyanin, a blue-coloured respiratory proteid, and the freshly shed blood is indigo in colour. The corpuscles are oval and large. The heart is a dorsal tube with seven chambers extending from the 7th to 13th segments. A pair of valvular ostia open into the anterior end of each chamber and a lateral artery leaves the posterior angle on each side. Posteriorly the heart is continued throughout the metasoma as a dorsal aorta. Anteriorly a truncus arteriosus (Fig. 522, 16)

leads forwards and soon divides into two, from each of which six vessels are given off to supply the prosomatic appendages, and other vessels to the brain and organs of the prosoma. Behind the point where it splits the truncus arteriosus gives off a right and a left branch which encircle the alimentary canal and fuse in the middle line ventrally; these vessels are then continued backward as a supra-neural artery which is in close contact with the ventral nerve-cord (Fig. 520, 7).

The blood system of *Scorpio* is better developed than is usually the case in Arthropods. The arteries end in minute channels not to be distinguished from capillaries, and these debouch into veins or into spacious venous sinuses. Two of the largest of these sinuses lie in the median line, one dorsal and one ventral. The former is the space of the pericardium; its walls are fibrous and not fenestrated and the blood is returned to it by special veins, a pair in each somite, which bring the oxygenated blood back from the lung-books. From the pericardium it enters the ostia of the heart. The blood is collected for transmission to the gills by the ventral venous sinus, and the roof of this sinus is connected with the floor of the pericardium by seven pair of vertical veno-pericardiac muscles, a pair for each segment traversed by the pericardium. When these muscles contract the cavities of the respective sinuses are enlarged and blood rushes in; they must therefore play a considerable part in the distribution of the blood through the system.

The pulmonary sacs, of which there are four pairs, communicate with the outer air by slit-like stigmata placed obliquely on the sternal plates of segments 9 to 12 (Fig. 519). Each of them contains from 130 to 150 lamellae or leaves, which constitute the so-called lung-books (p. 801). The leaves are borne on a definite axis and part of the edge of each leaf adheres to the wall of the respiratory chamber, only a small part of the edge being free. Each leaf is hollow and the blood to be oxygenated flows within the thin, slit-like cavity only separated from the air by the membranous walls.

The nervous system of *Scorpio* consists of a supra-oesophageal ganglion which supplies the median and marginal eyes and a very thickened and concentrated ring which embraces the oesophagus. This ring, with which is aggregated a number of post-oral ganglia, gives off paired nerves to the appendages of the

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first ten segments, and two ventral cords which, until they reach the 11th segment, bear no ganglia. This and the following six segments have ganglia, the last lying in the 4th metasomatic segment; behind this, nerves supply the last segment and the post-anal sting. The sense organs are the eyes; and since ridges exist in some species on the coxae of the pedipalps or of the 1st pair of legs, across which file-like surfaces can be drawn, forming very efficient stridulating organs, scorpions probably have some perception of sound.

The reproductive organs* are retiform, the annular shape which is common in the Arachnida having become, as it does in *Limulus*, a network. The ovary consists of three longitudinal hollow tubules united by transverse tubules. It lies ventral to the liver, and is embedded in or closely attached to that organ and is confined to the mesosoma. The oviducts are continuous with the walls of the ovary and pass forward and open by two pores on the genital operculum. The ova arise from certain cells lining the cavity of the ovary—the gonocoel—and when ripe project into it. They are fertilized in situ and the young scorpion begins its development within the ovary; after a time it passes into the oviduct and is ultimately born as a miniature of its parent. The scorpion therefore is viviparous and has no larval stage. The testis consists of two lateral tubules connected by transverse ducts. The vas deferens is modified distally to form an intromittent organ and it is provided with accessory glands. The spermatozoa are filiform and motile. The mother sometimes carries the young on her back.

The features which are mainly used in the systematic study of the scorpions are (i) the presence or absence of a tarsal spur or stout spine on the proximal tarsal segment of the last pair of legs; (ii) the single or double basal spur which arises from the soft skin between the last and the last but one tarsal segments; (iii) the nature of the spikes or hairs on the under surface of the last segment; and (iv) the shape of the sternum.†

Scorpions inhabit warm countries, some species burrowing in the sand. They shun the hot sunshine and live on insects

* The gonads and their ducts are coelomic; see p. 317.

† In the following systematic account we have followed Kraepelin, *Das Tierreich*, viii Lieferung, 1899.

and spiders, which they capture with their powerful pedipalps and sting to death with their poison sting. The metasoma is carried turned forward over the mesosoma when they run. The stories of their deliberately committing suicide when surrounded by a ring of burning coal are fabulous, though in their pain they lash their tails about and may wound themselves.

Geologically scorpions are very old though there are but few fossil representatives. *Palaeophonus*, apparently an aquatic form, in the arrangement of its walking legs and the number of its gnathobases is primitive. It and *Proscorpius* are Silurian, *Eoscorpius* Carboniferous and *Tityus* Oligocene.

There are 6 families amongst which are divided some 300 species, neglecting a good many doubtful ones.

Fam. 1. **Buthidae**. Triangular sternum (p. 801), narrowing anteriorly, basal spurs external and internal, the former often with an accessory spine. Tarsal spur often on 3rd as well as 4th pair of legs. Lateral eyes 3 or 5. *Buthus* with some 25 Old World species; *Parabuthus* African and Arabian; *Grospus* with but 2 species both from Madagascar; *Odonturus* East Africa and Madagascar, 2 species; *Butheolus* Mediterranean and Central and Southern Asia. The following six genera each have one species, *Microbuthus* from the Gulf of Aden; *Nanobuthus* E. Africa; *Charmus* Ceylon; *Stenochirus* Ceylon; *Isometroides* Australia; *Ananteris* Brazil; *Archisometrus* with 20 species from Asia, Africa and Australia; *Uroplectes* 16 species all African with the exception of one Oriental species; *Babycurus* 6 Central African species; *Isometrus* 6 cosmopolitan species; *Zabius* 1 S. American species; *Tityus* 30 American species; *Centrurus* 13 also New World species.

Fam. 2. **Scorpionidae**. Sternum with parallel or almost parallel sides, usually pentagonal. Basal spur only on outer side. No tarsal spur on 3rd and 4th legs. Lateral eyes 2 or 3. *Nebo* one Syrian and Arabian species; *Oculus* 1 species W. Indies; *Diplocentrus* 6 Neotropical species; *Urodacus* 6 Australian species; *Heterometrus* 12 Indian species; *Pandinus* 9 species from Africa and Arabia; *Scorpio* Mediterranean, Africa and Asia 2 species; *Opisthophthalmus* S. African with 29 species; *Hemiscorpion*, a single species Bagdad and Aden; *Hadogenes* 5 South African and Malagasy species; *Opisthacanthus* 8 species from Africa and America; *Cheloctonus* 3 S. African species; *Ischnurus* 1 species from some East African islands; *Hormurus* 2 species Oriental and Australian; *Iomachus* 2 Indian and East African species.

Fam. 3. **Chaerilidae**. An inner and an outer tarsal spur, two rows of bristles beneath the terminal lobe of the legs, which is not rounded. Two lateral eyes with a yellow spot behind. The prosoma narrows anteriorly. The movable claw of the chelicerae bears a row of low teeth and that of the pedipalps a row of obliquely overlapping ridges. Stigmata circular. Sternum as long or longer than broad, with a median groove ending in a pit. *Chaerilus* 5 Oriental species.

Fam. 4. **Chaetidae**. An inner and outer tarsal spur, terminal lobe not rounded. Often blind but when present the lateral eyes are two in

number. Movable claw of chelicerae very seldom toothed and then very weakly. Anterior end of prosomatic tergum not narrowed. The ridges or low spines on the movable claw of the pedipalp in a row, with scattered ones on one or on both sides of it. Stigmata often circular. Sternum as a rule no longer than broad. *Megacormus* 1 Mexican species; *Euscorpheus* 4 Mediterranean species reach North to the Tyrol and East to the Caucasus. The common Italian species is *E. italicus*. *Belisarius* 1 Pyrenean species; the following four genera are S. American, *Chactas* many doubtful species; *Broteas* 5 species; *Broteochactas* 4 species; *Teuthraustes* 3 species.

Fam. 5. **Vejoidea**. An outer and inner tarsal spur. Three lateral eyes. Sternum usually broader than long with a deep median furrow. Last tarsal joint of legs with a median row of hairs or papillae. Stigmata elongated. Median lamella of the pectines often moniliform. *Iurus* 1 cosmopolitan species; *Scorpiops* 4 species from the southern slopes of the Himalayas; *Uroctonus* 1 species from California; the following three genera are from southern North America, *Anuroctonus* 1 species; *Vejovis* 8 species; *Hadrurus* 1 species; *Hadruroides* and *Caraboctonus* both with 1 Neotropical species.

Fam. 6. **Bothriuridae**. The sternum consists of two narrow plates and is very much broader than long, it is scarcely visible. The middle lamella of the pectines is often moniliform. With the exception of *Cercophonius* all the genera are Neotropical. *Brachistosternus*, 2 species; *Thestylus* 1 species; *Urophonius* 2 species; *Bothriurus* 4 species; *Phoniocercus* 1 species; *Cercophonius* Australian with 1 species; *Centromachetes* 1 species.

Order 2. PEDIPALPI *

Arachnida with clawed non-chelate chelicerae and clawed or chelate pedipalps. The abdomen (meso- and meta-soma) may be stalked but is not universally so, it has eleven or twelve segments and sometimes bears a post-anal multi-segmented tail as in the Palpigradi. There are four lung-sacs. The anterior walking legs are much elongated and act as feelers.

The prosoma is usually covered by a single dorsal shield which bears anteriorly two median eyes and two groups of three lateral eyes, but some species are blind. Ventrally between the legs are sternal pieces called the pro-, meso-, and meta-sterna. The two pair of lung-books lie near the posterior border of the second and third mesosomatic sterna. The chelicerae, which have but two joints, are always provided with claws, and probably, as in the spiders, contain a poison-gland, since the bite of these animals is much feared. The bases of the chelicerae can be retracted into the cephalothorax. The pedipalps, as the name

* Kraepelin *Scorpiones u. Pedipalpi, Das Tierreich*, 8 Lff., 1899, M. Laurie, *J. Lin. Soc.*, London, xxv, 1894, p. 20. Bernard, *Tr. Lin. Soc.*, London (2), vi, 1894-97, p. 305.

of the Order suggests, are large and conspicuous. The coxae of the pedipalps are produced in towards the mouth. The various spines and hairs on its several segments are of systematic import.



FIG. 523.—*Admetus pumilio*. Kt Pedipalpi; Gb flagelliform anterior leg.

The first pair of ambulatory legs are produced into a long multi-segmented flagellum or whip which is tactile in function. The remaining legs bear a pair of claws and a soft process the “pulvillus” is present between the claws in some cases.

We know comparatively little of the internal anatomy of the Pedipalps. The mouth of *Thelyphonus* opens into a pharynx which is provided with muscles whose contraction enlarges its lumen; this passes into a narrow oesophagus which pierces the nerve mass and enlarges into the mid-gut. This gives off two lateral digestive glands which split up into five follicles and two median diverticula which are said to pass through the endosternite. In the abdomen the mid-gut gives off the voluminous “liver” which communicates by four paired openings with its lumen. Posteriorly the mid-gut bears a large stercoral pocket which receives at one end or the other the paired malpighian tubules.

Coxal glands are also well developed and lie under the endosternite. Their external opening is still to seek; if it exists it is probably in the neighbourhood of the third appendage.

The heart is elongated with two pairs of ostia in the prosoma

and seven behind. The respiration is carried on by the two pair of lung-sacs mentioned above. The nervous system is very concentrated and a median nerve which traverses the meso- and meta-soma is said to expand posteriorly into a ganglion.

There is a well developed but a symmetrically placed pair of "stink-glands" with reservoirs, whose ducts open with or near the anus. The last segment of the body, which with one or two others is narrowed and cylindrical, bears some light spots variously interpreted as eyes or olfactory organs, but at present the allocation of functions to these organs is purely conjectural.

The reproductive organs are paired, and the male has well-developed vesiculæ seminales. The group is as far as is known oviparous, and the eggs are embedded in a gelatinous mass which is carried about on the ventral surface of the abdomen of the mother which becomes arched or concave to receive the ova. The young emerge from the egg as miniatures of their parents.

The Pedipalpi are predaceous, living chiefly on insects. They inhabit the warm parts of the globe in both hemispheres. *Phrynus* is found in the Tertiary strata and a genus known as *Geralinura* in the Carboniferous. They are classified in two tribes, three families and twenty-two genera with some sixty to seventy species.



FIG. 524.—*Thelyphonus giganteus* (Koch). *a* Pedipalpi; *b* movable fang or claw forming with *c* claw on 4th joint, *a* didactyle claw; *d* claw on 3rd joint; *f* segmental elongation of abdomen supporting tail; *g* tail; *h* chelicerae; *m* eyes; *e* first palpal joint, with characteristic denticulations.

Tribe 1. UROPYGI.

Prosoma longer than broad; meso- and meta-soma 11-12 segmented, the last three segments narrow and cylindrical bearing the post-anal tail.

Fam. 1. **Thelyphonidae**. Prosomatic tergum of one piece. Tail long and multi-segmented, tarsus with two claws (Fig. 524). *Mimoscorpis* with one species from the Philippines; *Typopeltis* 4 species from China and the Amur; *Abalius* with 3 species from New Guinea and the South Sea Islands; *Tetrabalius* with 2 Mollican and Bornean species; *Thelyphonus* with 17 Oriental species; *Mastigoproctus* with 4 New World species;

Uroproctus with 1 Indian species; *Thelyphonellus* with 1 South American species; *Labochirus* with one species from Ceylon; *Hypoctonus* with 6 species from Further India and Borneo.

Fam. 2. **Schizonotidae**. Cephalothorax divided into two unequal parts by a transverse furrow, the posterior of which bears the 3rd and 4th ambulatory limbs; abdomen of 8 broad and three narrower segments, tail unjointed. *Schizonotus* 2 species from Ceylon and Liberia; *Trithyreus* 2 species from Burmah and the Bismark Archipelago.

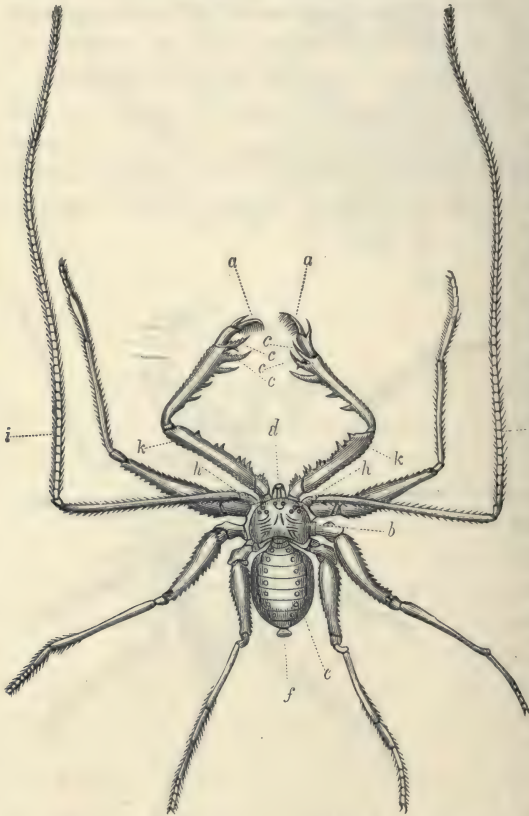


FIG. 525.—*Charon medius* (Koch). *a* Movable fangs or claws on fourth joint of pedipalpi (*k*), forming with claws (*c*) on third joint a modified didactyle claw; *b* thorax; *d* chelicerae; *e* abdomen; *f* button at end of abdomen; *h* eyes; *i* long antenniform legs.

Tribe 2.
AMBLYPYGI.

Cephalothorax broader than long, abdomen of 11 segments without tail.

Fam. 1. **Tarantulidae** with the characters of the tribe. *Phrynichus* 2 species from India, Ceylon and E. Africa; *Damon* 2 African species; *Acanthrophrynus* 1 species from Mexico and California; *Tarantula* 4 species from Texas and California through northern S. America; *Admetus* (Fig. 523) 1 S. American sp.; *Charon* 1 species from S.E. Asia and the Pacific Islands;

Stygophrynus 1 Burmese species; *Charnius* 3 species from South Sea Islands and the Seychelles; *Sarax* 2 species from E. Indies and Borneo; *Catagius* 1 Burmese species.

Order 3. ARANEIDA (ARANEAE) *

The cephalothorax (prosoma) covered by a single tergal shield, but a groove or line indicates the limits of the head; eyes usually eight or six; abdomen (mesosoma and metasoma) pedicellate, soft, with very rarely any trace of segmentation; two to four pairs of

spinnerets; sternum of two pieces; chelicerae two-jointed, non-chelate, with a poison gland; pedipalps modified in the male in connexion with fertilization.

The true spiders form a very large and widely distributed assemblage of



FIG. 526.—*Dysdera cambridgei* from the ventral side. *Kf* Chelicera; *Kt* pedipalpus; *K* basal joint (jaw) of pedipalpus; *P* lungs; *St* stigma of lungs; *St'* posterior stigma leading into the tracheae; *G* genital opening; *Sp* Spinnerets.



FIG. 527.—Poison gland and terminal joint of chelicera of *Avicularia* (*Mygale*). *K* Claw; *Gd* poison - gland; *B* poison vesicle.

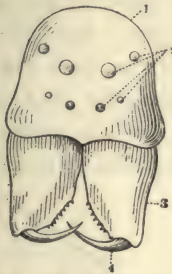


FIG. 528.—Front view of the head of a Spider, *Tetriz denticulata*, magnified (from Warburton). 1 Head; 2 eyes; 3 basal joint of chelicerae; 4 claw of chelicerae.

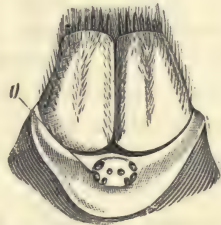


FIG. 529.—Anterior part of the cephalothorax of *Avicularia* (*Mygale*) with the eyes (O).

* C. L. Koch, *Die Arachneiden*, Nürnberg, 1839-48. Blackwall, *Spiders of Great Britain and Ireland*, Ray Society, 1861. Menge, *Preussische Spinnen*, beginning 1866. Thorell, *Genera of European Spiders*, 1869. Id. *Synonyms of European Spiders*, 1870-73. Simon, *Arachnides de France* (still incomplete) beginning 1874. Pickard-Cambridge, *Spiders of Dorset*, 1879-81. McCook, *American Spiders and their Spinning-work*, Paris, vol. i, 1889 (Philadelphia). Simon, *Histoire Naturelle des Araignées*, 2nd ed. vol. i, 1892, Paris. Peckham, *Sexual Selection in Spiders*, Nat. Hist. Soc. Wisconsin, 1889.

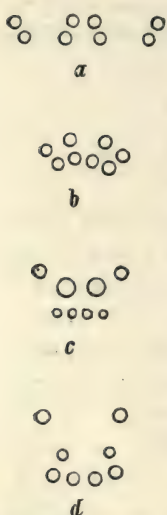


FIG. 530.—Arrangement of the eyes in different spiders (after Lebert). —a *Araneus* (*Epeira*); b *Tegenaria*; c *Dolomedes*; d *Salticus*.

animals, easily recognized by their stalked abdomen and by the presence of the spinnerets. The prosoma, often called the cephalothorax, bears the eyes, never more than eight, and usually in two transverse rows, each consisting of a pair of median eyes with a lateral eye on each side (Figs. 528, 530). Ventrally there is the sternum in two pieces (Fig. 526), the posterior being much the larger and separating the points of origin of the right and left legs. The abdomen is often globular but may be cylindrical or may assume many bizarre shapes. In some cases it is strengthened by sclerites and in the genus *Liphistius* there are seven of these dorsally and they here have a segmental value.

The chelicerae are two-jointed, the end-joint being a rather sickle-shaped claw which bears near its point the orifice of the duct of the poison gland (Fig. 527). It is this claw that poisons the prey of the spider. The pedipalps are of fair size with six joints; the coxa bears a gnathobase or "maxilla" which projects towards the mouth. In the male the terminal joint appears after the last moult in a very modified condition known as the palpal organ (Figs. 531, 533). This contains a vesicula seminalis, and spiders have been observed to first deposit their semen on part of a web and then to suck it into this vesicula seminalis and then to deposit it by the palpal organ on or in the female orifice, an operation not unattended with danger, as the larger female sometimes seizes and devours the small male. The eight legs have seven

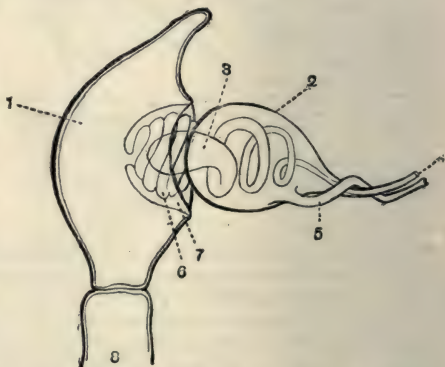


FIG. 531.—Diagram of palpal organ. 1 tarsus; 2 bulb; 3 vesicula seminalis; 4 opening of vesicula seminalis; 5 conductor; 6 haematodocha; 7 alveolus; penultimate joint of the pedipalp. After Warburton.

joints and end in two, or in three claws; the metatarsus or joint before the tarsus of the 4th leg bears in some forms a brush-like series of hairs, the *calamistrum* (Fig. 532), which are correlated with the presence of an accessory spinning organ, the *cribellum* (Fig. 535).

Most spiders breathe by means of two lung-books, which open by stigmata situated one on each side of the genital pore on the anterior ventral surface of the abdomen (Fig. 526). Each stigma leads into a space which is largely filled by a series of leaf-like plates resembling the leaves of a book. Within the substance of these plates the

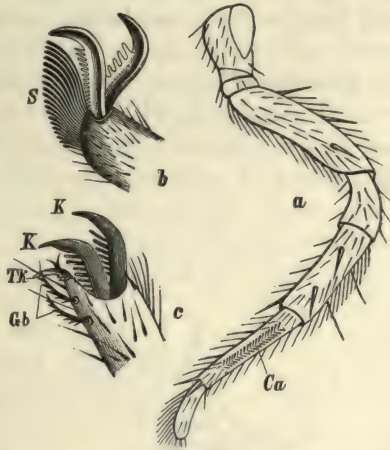


FIG. 532.—a Leg of the fourth pair of *Amaurobius ferox*; Ca calamistrum; b end of foot of *Philaeus chrysops* with two claws and pencil consisting of spatulate hairs (S); c end of foot of *Epeira diademata*; K web-claws; Tk ambulatory claw; Gb toothed bristles (accessory claws) (after O. Hermann).

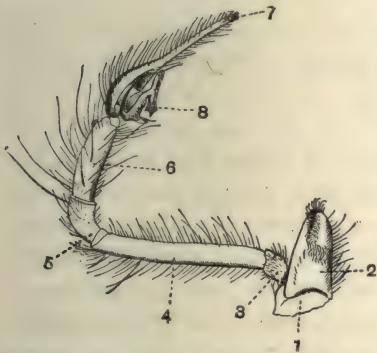


FIG. 533.—Pedipalp of *Tegenaria guyonii*, the large house-spider. 1 Coxa; 2 gnathobase, the so-called "maxilla"; 3 trochanter; 4 femur; 5 patella; 6 tibia; 7 tarsus; 8 palpal organ. After Warburton.

blood circulates whilst the air plays between neighbouring plates, and thus the blood is aerated. If, as in the Theraphosae, there be four lung-sacs the second pair lie close behind the first. From the developmental history of the scorpion there is little doubt that these lung-sacs represent highly modified appendages, perhaps something like the gill-bearing appendages of *Limulus* which

have sunk into the body (p. 801). When only one pair of lung-books is present, there is generally a tracheal system consisting of two or four main tracheae which open by two

or four stigmata, or by one median stigma, the result of the fusion of two primitive stigmata, just in front of the spinnerets. This tracheal system is usually regarded as a development of two lung-books or as having arisen independently within the group (see p. 776), and not as being genetically connected with the tracheae of insects. The tracheae connected with one stigma do not communicate with those connected with any other stigma, and they do not ramify throughout the body. Each stigma gives off a bunch of comparatively short tracheae which end blindly.

The male and female generative orifices (Fig. 526) only become visible after the last moult. As a rule they are difficult to see, but in the females of some families, e.g. the Dysderidae



FIG. 534.—Male and female of *Liryphia*, during copulation (after O. Hermann).

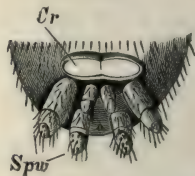


FIG. 535.—Spinning organ of *Amaurobius ferox* (after O. Hermann). *Cr* Cribellum; *Spw* spinning mammillae.

and Epeiridae the orifice opens on a complicated armature, the "epigyne," which is of considerable systematic importance. At the posterior end of the abdomen is a cluster of spinnerets (Figs. 535, 537) which may be two or four in number but are more usually six or eight, two anterior, two median and two posterior, and close behind the last is the anal tubercle bearing the anus and terminating the abdomen. The spinnerets are probably highly modified segmental appendages. They are very mobile and have at least two joints and they are pierced at their somewhat flattened end by innumerable minute pores through which the viscid fluid, which quickly hardens in the air into silk, exudes. This fluid is secreted by various glands and the excretions of the several glands differ in composition and functions. The pores open on the ends of minute projections termed *pusulae*. In some spiders grouped by Simon into the Cribellatae, there is, besides the spinnerets and in front of them, a double plate pierced by pores called the *cribellum*

(Fig. 535, *Cr*) ; from this silk also issues and its presence is always correlated with that of the calamistrum on the last pair of legs.

Some spiders have the power of making sounds and these are produced by certain comb-like structures being drawn over



FIG. 536. — The Garden Spider, *Araneus (Epeira) diadematus*, sitting in the centre of its web (after Blanchard).

others of a file-like nature. These stridulating organs are situated either between the cephalothorax and abdomen or between the chelicerae and the pedipalps or between the pedipalps and the anterior legs, all parts of which are movable upon one another.

Spiders take only liquid food and the mouth is minute and very difficult to find, being concealed by an under-lip or labium. It opens into a fine oesophagus which runs dorsalwards and dilates into a large sucking-stomach (Fig. 537, 2). The whole of these structures are lined by chitin and are stomodaeal. From the walls of the stomach stout muscles run to the tergum of the cephalothorax and to the endosternite, a plate-like endoskeleton which underlies the stomach. When these muscles contract the lumen of the stomach is enlarged and fluid is sucked into it. The stomach

opens into the endodermic portion (mesenteron) of the alimentary canal. This gives off, whilst still within the cephalothorax, two lateral diverticula each of which gives origin to five caeca (Fig. 537, 8). The caeca of the anterior pair pass forward towards the head and in a few cases they are known to fuse together. The posterior four pairs of caeca pass into the four pairs of coxae of the legs and sometimes turn back again and end under the nerve-mass (8). They do not anastomose. The mesenteron is then continued as a spacious tube through the abdomen where it receives the ducts (3) of a large "liver" which occupies a good deal of the space of the abdomen; finally it opens into a rectum which bears dorsally a large stercoral pocket or sac (5) in which the faeces accumulate. The rectum ends in the anus; it is

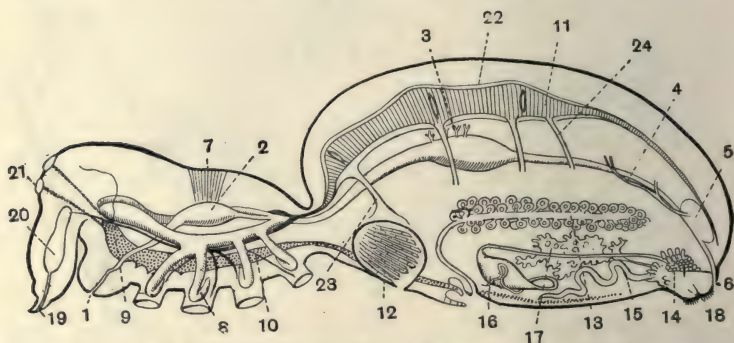


FIG. 537.—Diagram of a Spider, *Araneus (Epeira) diadematus*, showing the arrangement of the internal organs \times about 8. 1 Mouth; 2 sucking stomach; 3 ducts of liver; 4 malpighian tubules; 5 stercoral pocket; 6 anus; 7 dorsal muscle of sucking stomach; 8 caecal prolongation of stomach; 9 cerebral ganglion giving off nerves to eyes; 10 sub-oesophageal ganglionic mass; 11 heart with three lateral openings or ostia; 12 lung sac; 13 ovary; 14 acinate and pyriform silk glands; 15 tubuliform silk gland; 16 ampulliform silk gland; 17 aggregate or dendriform silk glands; 18 spinnerets or mammillae; 19 distal joint of chelicera; 20 poison gland; 21 eye; 22 pericardium; 23 vessel bringing blood from lung sac to pericardium; 24 artery. (From Warburton.)

lined with chitin and is proctodaeal in origin. Just where the mesenteron unites with the proctodaeum a pair of malpighian vessels (4) pour their secretion into the intestine. The various investigators who have described the development of spiders are not in accord as to the origin of these excretory tubules, but the most definite account attributes them to the mesenteron.

Coxal glands, which are excretory in function and which are believed to represent nephridia opening on the one hand into an end-sac and on the other to the exterior, are well developed in some spiders, e.g. the common house-spider, *Tegenaria derhamii*,

but reduced in others. They open on the third pair of legs in the young and traces of other paired openings have been found in the young of *Atypus* on the first and second legs.

The heart (11) is abdominal in position, dorsal and in some species concealed by the "liver" tissue. It lies in a distinct pericardium (22) and has three pair of ostia opening into it. Posteriorly it gives off a caudal artery, laterally three pair of arteries which supply the abdomen, and anteriorly an aorta which gives blood to the cephalothorax. The arteries are fairly well developed in spiders, but there are no capillaries, and the blood ultimately finds its way into sinuses, of which three chief ones in the mesosoma conduct the blood to the lung-books where it is aerated. There are also three in the abdomen which lead the blood in the same direction. From the lung-books the blood returns to the heart by pulmonary veins.

The spinning glands lie in the abdomen and in the most complete state consist of five kinds, (i) ampulliform (16) which open on the anterior and median spinnerets, (ii) aggregate glands (17) which open on the posterior spinneret, (iii) tubuliform glands (15) which open on the middle and posterior spinneret, (iv) piriform glands (14) which are numerous and open on the anterior and posterior spinnerets, and (v) some hundred aciniform glands which open on the median and posterior spinnerets. In those spiders which possess a cribellum, it is supplied by a sixth set of (vi) cribellum glands. These various glands supply different kinds of threads which together make up the web of a spider. For instance the ampulliform glands supply the first framework and the radial lines of the geometric webs. The spiral lines are each double and they are believed to be formed by the aciniform glands, and the viscid fluid, which owing to some physical law arranges itself in regular beads on them, is said to originate from the aggregate glands. The tubuliform glands give rise to the silk of which the egg-cocoon is made, and the pyriform glands form the foundation lines and the attachment discs, which run from the web to surrounding objects and serve to glue together such of the non-viscid lines as the spider wishes to connect.

A spider has apparently no power to cease secreting silk as long as it is being drawn from its body, and the legs are used for cutting the thread as soon as enough has emerged. The legs are

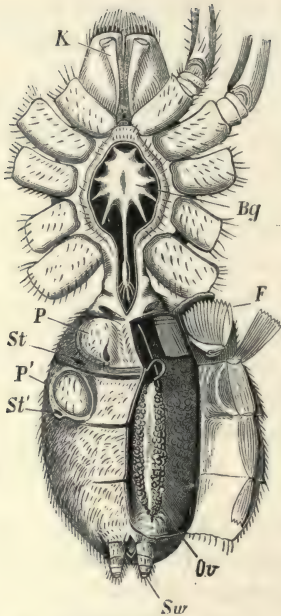


FIG. 538.—*Arvicularia*, ventral side, part of the skin is turned aside. *K* Chelicera; *Bg* thoracic ganglionic mass; *P*, *P'* lungs; *F* lamellae of the lungs; *St*, *St'* stigmata; *Ov* ovary; *Sw* spinnerets.

also well adapted for running lightly on the threads. There are a very great number and variety of webs and snares built by spiders which it is impossible to even enumerate here, but mention must be made of certain streamers of silk which the young spiders, having previously ascended to a rail-top or some such place of vantage, let out of their spinnerets; the wind catching these, as it might a parachute, wafts the spider into the air and often carries it considerable distances. These streamers form the so-called gossamer, the origin of which was for a long time a mystery.

The nervous system is very concentrated; there is a supra-oesophageal ganglion supplying the chelicerae and the eyes, and a large star-like infra-oesophageal mass supplying the rest of the

appendages and the body (Fig. 537, 9, 10, Fig. 538). Between the two passes the minute oesophagus.

The generative organs lie concealed amongst the branches of the "liver." The testes (Fig. 539) are two cylindrical organs opening into coiled vasa deferentia which unite to open by a single aperture at the anterior ventral end of the abdomen.

The ovary is annular and the eggs project from the surface of the gland (Fig. 537, 13). Anteriorly the ovary passes into short oviducts which act as spermathecae; they open separately and the opening may be protected and complicated by an "epigyne." Spiders prepare either nests or cocoons for their young, and the latter are sometimes carried about for a time by

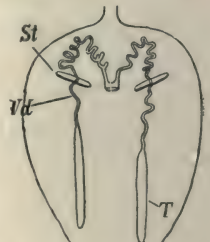


FIG. 539.—Sexual organs of a *Tegenaria domestica*, with the abdomen in outline (after Bertkau). *T* testis; *Vd* vas deferens; *St* stigma.

the female either clasped in the chelicerae, e.g. *Dolomedes*, or attached to the abdomen as in *Lycosa*. The mother often exercises a certain amount of parental care over her offspring.

A few forms, e.g. *Protolycosa*, and *Palasanea*, occur in the coal measures, but the greater number of fossil forms occur in the amber of the Oligocene.

The spiders form a very large group and a very homogeneous one, so that the difficulties of classification are great. We have in the main followed Simon (*op. cit.* on p. 811). The first three families mentioned below are separated by Simon as the group Araneae Theraphosae from all the other spiders which he calls Araneae Verae.

Sub-order 1. ARANEAE THERAPHOSAE.

Chelicerae directed in front, two pair of pulmonay sacs, often 4 spinnerets, no gnathobase on pedipalps.

Fam. 1. **Liphistiidae**. Abdomen segmented dorsally, with a series of terga; spinnerets, eight in number, situated about halfway along the abdomen; 4 lung-books; 8 eyes on an elevation. *Liphistius* the only genus, with but 2 species: one from Sumatra, and one from Penang.

Fam. 2. **Aviculariidae (Mygaliidae)**. (Fig. 538.) Cephalothorax oval or almost square; eyes usually 8, rarely 6; chelicerae independent of one another with great vertical movement; no gnathobase on pedipalps which are leg-like; 4 stigmata and 4 spinnerets. Terminal joint of the chelicerae or unguis folded down into a groove of the sub-terminal joint. The Aviculariidae include the large tropical spiders as large as mice and also the trap-door spiders of the warmer temperate regions. They are divided into 7 sub-families: i. **Paratropidinae**, with two American genera, *Paratropis* and *Anisaspis* with thick scaly or hairy integuments: ii. **Actinopodinae** with 3 genera, *Stasimopus* from South Africa, *Eriodon* from Australia, and *Actinopus* from South America makes cylindrical burrows with a trap-door: iii. **Miginae** with very short chelicerae, with three genera, *Moggridgea*, S. Africa, *Migas* S. Africa and N. Zealand, and *Myrtales* Madagascar: iv. **Ctenizinae**, these are the typical trap-door spiders and include some 40 genera, *Pachylomerus* widely distributed, *Conothele* Malaysia, *Cyclocosmia* America, *Acanthodon* widely distributed, *Cteniza* France and Italy, *Cyrtocarenum* Mediterranean, *Aporoptychus* Africa and America; *Cyrtacanthus* Africa; *Nemesia* the most common of the European trap-door spiders, Mediterranean: v. **Barychelinae**, *Barychelus* New Caledonia, *Leptopelma* Italy and Africa, *Sason* Andaman Islands: vi. **Aviculariinae**, *Ischnocolus* widely distributed, *Chaetopelma* Egypt, Syria and Arabia, *Crypsidromus* America, *Phlogius* South-west Asia, *Selenocosmia* East Indies, *Theraphosa* Central America, *Homœomma* Brazil, *Eurypelma* America, *Avicularia* America, *Poecilotheria* India: vii. **Diplurinae**, these weave webs but do not make tunnels, *Diplura* is American, *Brachythele* and *Macrothele* are European.

Fam. 3. **Atypidae**. Six spinnerets; terminal joint of chelicerae or unguis does not fold down into a groove of the subterminal joint, males

differ markedly from females. This family is nearly related to the preceding and seems to represent it in the cooler regions of the earth. They are mostly stoutly built and smooth. There are but 6 genera. *Brachybothrium*, *Atypoides* and *Hexura* are American, *Mecicobothrium* from Argentina, *Calommata* Asia and *Atypus* European. The last named has 2 British species, *A. piceus* and *A. beckii*; both occur in the southern half of the country, but the latter is very rare. *A. piceus* makes a tubular nest lined with web in the earth, the web often projects.

Sub-order 2. ARANEAE VERAЕ.

Chelicerae directed vertically or obliquely downwards, with lateral action, one pair of pulmonary sacs, and tracheae with one pair of tracheal stigmata, six spinnerets, a gnathobase on the pedipalps.

Section I. CRIBELLATAE.

Fam. 4. **Hypochilidae.** Four pulmonary sacs, an exception to the characters of the sub-order; the male is hardly a third the size of the female. Two genera *Hypochilus* America and *Ectatosticta* China.

Fam. 5. **Uloboridae.** Eight eyes, with one exception in 2 curved lines; legs usually long and robust and very unequal in size, the anterior being by far the longest; 3 tarsal claws; anal tubercle long. The spiders of this family are clothed with squamous hairs. Seven genera. *Dinopis* and *Menneus* are both tropical, *Uloborus* widely distributed, *Sybota* Mediterranean and American, *Hyptiotes* Europe and America, *Myagrammopes*, widely distributed, *Aebutina* Brazil.

Fam. 6. **Psechridae.** Legs of very unequal length, three claws and a tuft of hairs. Sedentary spiders which weave very large webs. *Psechrus* with 2 species and *Fecenia* with 5 or 6 are both from Malaysia.

Fam. 7. **Zoropsidae.** Scopulae or brushes of hairs on the tarsi and metatarsi; legs about the same size, cribellum and, especially, the calamistrum not well developed. *Acanthoctenus*, Central and South America, *Zoropsis* Mediterranean and Canaries, *Zorocrates* America, and *Raccius* Ethiopian.

Fam. 8. **Dictynidae.** Cephalothorax oval, the cephalic portion large; eyes in two almost parallel rows; chelicerae long and robust; legs moderate and about equal in length. These are sedentary spiders constructing a rather irregular web with no retreat into which the owner can retire. There are 16 genera, widely distributed, *Amaurobius* (Figs. 532, 535) is British, *Nurscia* Central Asia, *Lathys* and *Dictyna* Old and New World.

Fam. 9. **Ecobiidae.** Cephalothorax reniform; sternum very large; chelicerae small and feeble; anal tubercle large and with 2 joints. *Ecobius* with some 15 species is the only genus, mostly tropical and sub-tropical, though they spread into the Mediterranean district. They usually live in deserts weaving their webs under stones, etc. Except for the cribellum they are allied to the Uroctidae.

Fam. 10. **Eresidae.** Cephalothorax thick; cephalic portion large; eyes arranged in two squares one inside the other; chelicerae robust; legs short; large cribellum; exoskeleton covered with thick hairs. *Stegodyphus*, widely spread in the Old World, builds its web in bushes. The remaining four genera which are mainly African, *Adonea*, *Dresserus*, *Dorceus* and *Eresus*, build their webs on the ground.

Fam. 11. **Filistatidae.** Cephalothorax oval and elongated; eyes

crowded together; chelicerae small; integument with few hairs; two pulmonary sacs and two minute widely separated tracheal stigmata just behind them; legs of male long and slender. The single genus *Filistata* includes some 15 species widely distributed, a few are Mediterranean.

Section II. ECRIBELLATAE.

No cribellum or calamistrum.

Fam. 12. **Sicariidae (Scytodidae).** Eyes six; legs longish and slender; spinnerets small and crowded together; integument smooth; palpal organ in male simple. This family lives in outhouses and under débris. *Plectreurus* American, *Periegops* New Zealand, *Sicarius* Africa and America, *Loxosceles* and *Scytodes* widely distributed, the latter has one species *S. thoracica* which has occasionally been found in the South of England, *Drymusa* Africa.

Fam. 13. **Leptonetidae.** Cephalothorax short and rounded, large; eyes absent or 6 small ones; chelicerae long and attenuated; legs usually long and slender; spinnerets nearly equal in size. Small spiders with long legs; inhabitants of caves and caverns or vegetable refuse in forests. *Leptoneta* Europe, Africa and Japan, *Telema* caves in the Pyrenees, *Psilodermes* Luzon, *Usofila* America, *Ochyrocera* Asia and America, *Theotima* Philippines and Venezuela.

Fam. 14. **Oonopidae.** Cephalothorax shortly ovate; six eyes closely packed occupy almost all of the breadth of cephalic area; chelicerae conical; sternum well developed; legs moderate and usually equal in length; sexes the same size. There are very small spiders varying in length from 2-3 mm., they live in dry vegetable detritus, they run rapidly. There are 19 genera. *Orchestina* and *Oonops* are widely distributed. *O. pulcher* a small red-brick spider found in ditches represents the family in the United Kingdom. *Scaphiella* West Indies and Venezuela, *Epectris* Philippines.

Fam. 15. **Hadrotarsidae.** Eight eyes, two large ones central and three small ones in a row on each side in front; chelicerae small and feeble; sternum very large; 4 spinnerets; legs very short. Minute spiders with but 2 species *Hadrotarsus babirussa* found on an island near New Guinea and *Gmogala scarabaeus* found near Sydney.

Fam. 16. **Dysderidae.** Cephalothorax oval sometimes elongate; eyes six; chelicerae robust; abdomen elongate almost cylindrical; spinnerets short; palpal organ of male simple; integument smooth. This family has 2 sub-families: (i) **Dysderinae** in which the sternum is produced upwards between the legs towards the carapace. *Rhode* Mediterranean, *Harpassa* and *Holissus* Corsican, *Harpactes* and *Dysdera* have British species, *Tedia* Syrian, *Stalita* in caves in Dalmatia, and *Orsolobus* American. (ii) **Segestriinae**, with 2 genera, *Segestria* represented in England and *Ariadna* widely distributed and the only genus of this family which frequents the Tropics.

Fam. 17. **Caponiidae.** Cephalothorax oval; legs short; the spinnerets are arranged in two lines, the median being pushed forward and lying between the anterior; no pulmonary sacs, these structures being replaced by tracheae. 3 genera, *Nops* and *Caponina* Central and South America, West Indian Islands, and *Caponia*, Africa.

Fam. 18. **Prodidomidae.** Eyes eight, the 4 anterior in a straight line; chelicerae very robust; legs short; abdomen oval and elongate. Small

spiders 2-4 mm. found under stones and in dry situations. *Prodidomus* widely distributed, *Eleleis* Africa, and *Zimiris* Southern Asia.

Fam. 19. **Drassidae**. Oval cephalothorax rather flat; 8 eyes in two transverse lines; chelicerae vertical; legs with spines, two claws and a scopula. Simon divides this family in 4 sub-families: (i) **Hemicloëinae**, *Hemicloea*, *Hemicloëina*, *Pyrnus* and *Rebilus* New Holland and the former also from New Zealand, etc. (ii) **Drassodinae**, *Theuma* Asia, *Anagraphis* Africa, *Lygromma* America, *Tricongius* America, *Drassodes* cosmopolitan, *Echemus* widely distributed, *Lampona* New Holland, *Laronia* America and Africa, *Gnaphosa* Europe, Africa and America. (iii) **Cithaeroninae**, *Cithaeron* Asia and Africa. (iv) **Cybaeodinae**, *Cybaeodes* Corsica and France, *Andromma* Africa.

Fam. 20. **Palpimanidae**. Cephalothorax variable; 8 eyes in two transverse rows separated from anterior edge by a band; sternum oval projecting between the thighs and so forming articular cavities; anterior legs thick; abdomen oval or long. Three sub-families: (i) **Stenochilinae** with *Metronax*, *Stenochilus* and *Colopea* all from the far East. (ii) **Huttoniinae** with *Huttonia* from New Zealand. (iii) **Palpimaninae**, *Anisaedus* S. America, *Chedima* Morocco, *Palpimanus* Mediterranean, and others.

Fam. 21. **Zodariidae**. Cephalothorax convex and rounded in front; chelicerae very robust; sternum large and flat; tarsi usually 3-clawed. This is a heterogeneous assemblage of exotic forms divided into five sub-families: (i) **Homalonychinae** with the American *Homalonychus*. (ii) **Storenomorphinae** with *Storenomorpha* Burmah and Madagascar, and others. (iii) **Cydrelinae** with *Cydrela* which lives in sand in Africa, and others. (iv) **Cryptothelinae** with *Cryptothele* from Seychelles and the East Indies; this genus has the power of retracting its spinnerets. (v) **Zodariinae** with *Zodarion* and many other genera.

Fam. 22. **Hersiliidae**. This family is a peculiarly distinct one, showing little affinity with any other. The cephalothorax is at least as broad as long; usually eight eyes with the anterior laterals smaller than the others; chelicerae rather feeble; legs long and slender, 3 clawed; the posterior spinnerets are very long and 2-jointed. They are active spiders living on bark, etc. in Africa. *Hersilia*, *Hersiliola*, *Tama* and *Murricia*.

Fam. 23. **Urocteidae**. Cephalothorax broader than long; 8 eyes crowded together; chelicerae weak; legs shortish and stout and of equal length; abdomen large, oval and depressed; posterior spinneret long. *Uroctea* Mediterranean and China and Japan. There is a strong resemblance between the Urocteidae and the Cribellate family *Oecobiidae*.

Fam. 24. **Ammoxenidae**. Cephalothorax as in *Hersiliidae*; eyes compact; coxae highly developed; tarsi very long, 2 clawed; abdomen large; *Ammoxenus* Africa.

Fam. 25. **Pholcidae**. Cephalothorax short and rounded; the median anterior eyes are black, separated from the group of others which are white and sometimes stalked; legs extremely long and slender, the metatarsus and tarsus being greatly elongated and with additional "false" joints. Sedentary spiders, spinning webs under stones, in outhouses, etc. Two sub-families: (i) **Pholcinae**, *Artema* Africa and Asia, *Pholcus* almost cosmopolitan. *P. phalangioides*, the only British species, is common in the South in deserted buildings, *Leptopholcus* Africa, *Smeringopus* tropical, *Priscula* S. American, *Blechnroscelis* America, *Modisimus* West Indies. (ii) **Ninetidinae**, *Ninetis*, the sole genus, Arabia.

Fam. 26. **Theridiidae**. Spinnerets of equal length; tarsi with 3

pectinated claws; chelicerae usually narrow. The group is an enormous one and with few exceptions it consists of sedentary spiders which capture their prey not by running after them but by snaring them in webs. The webs are never orbicular but consist of an irregular webbing in the middle of which they hang with their ventral surface uppermost and escape their enemies by suddenly dropping down without making a thread. Some of them live semi-parasitically in the webs of other species. The cocoons are numerous and mostly rounded and silky. Simon divides the family into 18 groups: i. *Synotaxae* with *Synotaxus* from S. America. ii. *Argyrodeae* semi-parasitic with greatly elongated abdomen, *Argyrodes* and *Rhomphaea* both tropical and sub-tropical. iii. *Hetschkieae*, *Hetschkia* Brazil, *Mecynidis* Transvaal. iv. *Propostireae*, a single genus, *Propostira*, from Ceylon. v. *Moneteae*, again a single genus, *Moneta* from India and Africa. vi. *Spinthareae*, *Spintharus*. vii. *Episineae*, *Episinus* with a British species and widely distributed, *Janulus* America and the Indies. viii. *Oeteae*, *Oeta* Ceylon. ix. *Euryopeae*, *Euryopsis* widely distributed. x. *Sedasteae*, the only genus *Sedasta* is African. xi. *Theridieae*, *Theridion* with over 300 species, 17 of which are British, the commonest *T. sisyphium* swarms on holly and other low trees. xii. *Phoroncidieae*, with remarkable spines, *Phoroncidia* Africa and S. Asia, *Hyocrea* S. American. xiii. *Dipoenae*, *Dipena* cosmopolitan. xiv. *Pacullae*, *Paculla* East Indies. xv. *Asageneae* with highly developed stridulating organs, *Steatoda* Europe and America, has one British species common in angles and corners of walls, *Asagena* and *Lithyphantes* have also each a British species and *Teutana* two. xvi. *Histagonieae*, *Histagonia* Africa and America. xvii. *Theonoeae*, *Theonoe* France. xviii. *Pholcommateae*, *Pholcomma* Europe.

Fam. 27. **Argiopidae.*** Sedentary spiders which build an orb or wheel-like web; chelicerae much more powerful than in the preceding family; legs very variable, often armed with spines. There are 4 sub-families. 1. **Linyphiinae** with 3 groups: i. *Erigoneae*, a very large assemblage including the "money-spider" and those spiders which cover the fields with gossamer, over 100 species including species of *Erigone*, *Panamomops* are British; ii. *Formicineae*, as their name implies they look like ants, *Formicina* Mediterranean and the Japanese *Solenysa* form the group; iii. *Linyphiidae*, *Linyphia triangularis* is common in British gorse, *Tmetiscus* has some 20 British species and *Labulla*, *Bathyphantes*, *Bolyphantes* and *Lepthyphantes* are also represented in our Islands. 2. **Tetragnathinae.†** *Pachygnatha* lives amongst grass and does not weave an orb, there are 3 British species. *Tetragnatha* also with British representatives makes a wheel-like web; *Meta segmentata* is common in English gardens. There are many other genera. 3. **Nephilinae.** As a rule large spiders with great difference in size between males and females, *Phonognatha* Tasmania, *Nephila* tropical, etc. 4. **Argiopinae**, most of the spiders of this sub-family were formerly included in the great genus *Epeira*. *Argiope* and *Gea* and *Cyrtophora* tropical and sub-tropical; *Arachnura* Africa, Asia and

* Simon devotes 340 closely printed pages to this gigantic group; after describing the first three of his projected nine sub-families he abandons the attempt and classifies the rest of the family into twenty-eight sub-groups of the *Argiopinae*. We have mentioned but a minute proportion of the genera so grouped.

† This and the following two sub-families are almost identical with the old family *Epeiridae* now discarded by Simon.

New Zealand; *Cyclosa*, temperate and sub-tropical; *Mangora* Europe, Asia and America; *Bertrana* tropical America; *Araneus* (*Epeira*, Figs. 530, 536, 537) cosmop.; *Caerostris* Asia, Africa; *Gasteracantha* tropical; *Micrathena* tropical America; *Xylethrus* Central and South America; *Glyptogona* Mediterranean, Africa and America; *Anepsia* Malaynesia and Polynesia; *Hypognatha* Central America and Antilles; *Physiola* Venezuela; *Cyrtarachne* Africa, Asia; *Glyptocranium* America and Antilles; *Exechocentrus* Madagascar; *Poltys* Asia and Africa; *Celaenia* Tasmania, New Zealand; *Arcys* New Holland, Tasmania; *Dolophones* Ceram, New Holland; *Testudinaria* Peruvia; *Ursa* Africa and America; *Gnolus* S. America; *Theridiosoma* Europe, Asia and America; *Anapis* Africa and America.

Fam. 28. **Archaeidae.** A very distinct family of but two genera. The anterior portion of the cephalothorax, or caput, is separated from the posterior; the chelicerae are elongate; the silk-papillae are peculiar; *Archaea* Madagascar; *Mecysmauchenius* America.

Fam. 29. **Mimetidae.** The chelicerae are narrow, cylindrical, and parallel; abdomen convex and variable; in the genus *Gelanor* the pedipalps of the males are extraordinarily long; the spiders of this family make little use of their silk and construct no web, they live amongst plants and bushes. *Gelanor* Central America; *Ero* Europe, Asia, Africa and America; *Mimetus* Africa, India, New Zealand and America.

Fam. 30. **Thomisidae.** Called crab-spiders from their sideways gait. A very large family of varied forms. The cephalothorax is short; legs usually very unequal; the anterior two pairs larger and stouter than the others; there are five indurated spots on the upper surface of the abdomen.



FIG. 540.—
Misumena
vatia.

These spiders are wanderers, never weaving a fixed web; they capture their prey by their fleetness or by springing out on them from shelter in which their mimetic colours have concealed them. There are 6 sub-families: 1. **Aphantochilinae** with 2 genera *Bucranium* Central America and *Aphantochilus*, Venezuela and Brazil. 2. **Stiphropodinae.** *Stiphropus* Africa and S. Asia. 3. **Strophilinae,** *Cerarachne*, *Strophilus* both American. 4. **Misumeninae,** *Tagulis* Madagascar; *Apyre*, *Alcimochthes* Malaynesia; *Dieta* Africa and Asia; *Amyciaea* East Asia and Africa; *Mystaria* Africa; *Tmarus* tropical; *Talaus* Africa and E. Asia; *Pagida* East Indies; *Porrhopis* New Guinea and New Holland; *Bomis* New Holland; *Cymbacha* Tasmania and New Holland; *Camaricus* Africa and S. Asia; *Coriarachne* Europe, Asia and America; *Platythomisus* Africa and Malaynesia; *Thomisus* cosmopolitan; *Platyarachne* S. America; *Diaea* cosmopolitan, *Misumena* (Fig. 540) cosmop. 5. **Stephanopsinae,** *Hedana* Polynesia and S. America; *Stephanopoides* America; *Phrynarachne* Africa and S. Asia; *Stephanopsis* Madagascar, Malay, America. 6. **Philodrominae,** *Gephyra* Indo-China, *Philodromus* cosmopolitan.

Fam. 31. **Platoridae.** Cephalothorax very flat, chelicerae short; abdomen very flat; the anterior spinnerets are outside the median and thus widely divaricated; medium sized brown or yellowish spiders. Only 3 genera, *Plator* China, *Doliomalus* Chili; *Vectius* S. America.

Fam. 32. **Clubionidae.** Cephalothorax oval; chelicerae robust; legs more or less long and some longer than the others; the anterior spinnerets are contiguous. There are 7 sub-families: 1. **Selenopinae** *Selenops* cosmopolitan. 2. **Sparassinae,** *Sparassus* in all warm regions. 3. **Clubioninae,** *Clubiona* with 15 British representatives; *Chiracanthium*

with 3. 4. **Cteninae**, *Ctenus* in all warm regions. 5. **Liocraninae**, *Liocranum* Europe, Asia and America. 6. **Micariinae**, *Micaria* Europe, Asia and America. 7. **Corinninae**, *Corinna* Africa, Europe and Asia.

Fam. 33. **Agelenidae**. (Fig. 541.) Cephalothorax oval, caput distinguished from the thorax by lines; chelicerae convex and vertical; abdomen oval; the spinnerets pressed together; tarsi 3-clawed; legs unequal, the 3rd pair is the shortest. Sedentary spiders which weave large webs ending at one point or another in a cylindrical retreat. They are common in cellars and outhouses. There are 4 sub-families: 1. **Nicodaminae**, *Nicodamus* New Holland and Tasmania. 2. **Cybaeinae**, *Desis* is marine living amongst Madrepores in the Indian and Pacific Oceans, *Argyroneta* is the common water spider which lives in fresh-water throughout Europe and Asia. 3. **Ageleninae**, *Agelena* widely distributed is common in England as *A. labyrinthica* on the sides of banks and ditches; *Tegenaria* (Figs. 533, 542) cosmop. has 7 British species; *Coelotes*, also British, lives under stones. 4. **Hahniinae**, spinnerets arranged in one row, four or five species of the widely distributed *Hahnia* occur in our Islands.

Fam. 34. **Pisauridae**. Intermediate between the Agelenidae and Lycosidae. Hairy spiders with long legs; abdomen oval but rather pointed behind, the anterior spinnerets are very thick. There are numerous genera with few species. *Pisaura* (Fig. 543) Eur., Asia, Africa. *P. mirabilis* occurs in British woods and commons; *Dolomedes* with a like wide distribution occurs in the genus; *D. fimbriatus* in our marshes.

Fam. 35. **Lycosidae**. "The wolf-spiders" which pursue their prey by running, and carry the egg-cocoons attached to the under side of their abdomen. Cephalothorax longer than broad; abdomen oval and short; legs moderately long, the 4th pair being the longest; eyes in three rows. Many wolf-spiders form no retreat, others burrow in the ground. *Lycosa*, an enormous and cosmopolitan genus, including the true tarantula spiders, has some twenty British species; *Pardosa* with a similar distribution is also well represented in the United Kingdom.

Fam. 36. **Senoculidae**. Abdomen long; legs long and unequal; anterior spinnerets remarkably thick; three claws. This family contains only the South and Central American genus *Senoculus*.

Fam. 37. **Oxyopidae**. Cephalothorax narrows anteriorly; abdomen



FIG. 541.—An Agelenid Spider (*Cambridgea fasciata*, Koch). Adult male. 1-7 seven joints of leg.

like a spear-head; eyes very unequal; chelicerae long and pointed; legs long and not very unequal; integument soft with numerous coloured hairs. They are day spiders and run swiftly over plants and at times jump actively. *Peucezia* tropical; *Oxyopes* sub-tropical and tropical, one species is very rarely found in South England; *Tapinillus* tropical America.

Fam. 38. **Salticidae (Attidae).** The largest family of the Order with already some thousand recognized species. They are primarily tropical but extend north and south, some 33 species reaching Great Britain.



FIG. 542.—*Tegenaria domestica* ♀.



FIG. 543.—*Pisaura mirabilis* ♀.



FIG. 544.—*Salticus scenicus* ♀.

Cephalothorax longer than it is broad; eyes very unequal; chelicerae vertical; abdomen narrowing behind; legs short and robust, 2 claws; sexes usually of about the same size but differing in colour. The Salticidae are hunters both by running and jumping especially in the sunshine, and the males before mating indulge in various prenuptial antics. They form no snares but they weave a retreat in which the female sits and the eggs are protected. They are divided into some seventy-five groups of which we only mention a very few. **Marpiseae** with *Salticus* (Fig. 544) Eur., Asia, America outside the Tropics, *Marpissa* with the same wide distribution, and *Hytia* which does not occur in Asia. There are British representatives of these genera. **Sitticeae** with *Sitticus* (*Attus*) Europe, Asia and America, *S. pubescens* is often seen on walls and palings. **Hasariae** with *Hasarius* cosmopolitan in warm climates with a British species common in woods. **Mymarachneae** include spiders which mimic ants. *Myrmarachne formicaria* a cosmopolitan species in temperate climes is found, but very rarely, in England.

Order 4. PALPIGRADI*

Arachnids with a cephalothorax (prosoma) of four fused segments corresponding with the first four jointed limbs, and of the 5th and 6th segments which remain free; the abdomen (meso- and meta-soma) is stalked and narrowed behind; it is composed of eleven segments and bears a long multi-segmented appendage; the chelicerae are three-jointed; no eyes; the mouth is bounded by an epistome and a hypostome.

It is only within the last twenty years that the Palpigradi have been discovered and investigated. They fall into two genera, *Prokoenenia* and *Eukoenenia*. They are all minute, their total length being scarcely 1 mm. They are very widely distributed.

The prosoma consists of four fused segments corresponding with the four anterior limbs, viz. the chelicerae, the pedipalpi,

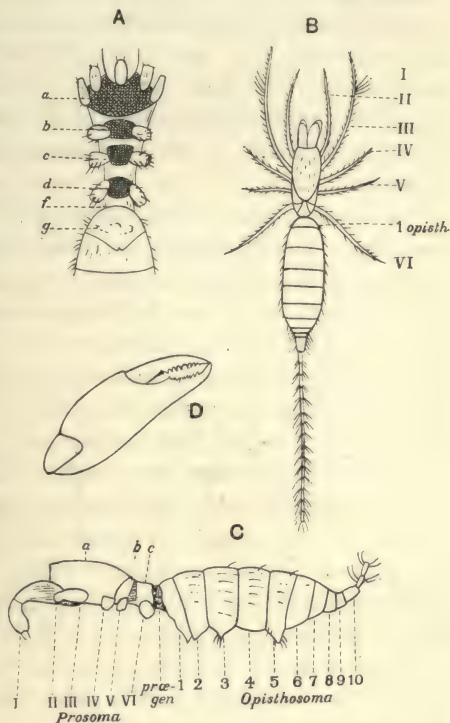


FIG. 545.—*Eukoenenia mirabilis*, Grassi, one of the Palpigradi. *A* ventral view of cephalothorax (prosoma) and of anterior region of abdomen (opisthosoma) with the appendages cut off near the base: *a* and *b* prosternites; *c* mesosternite; and *d* metasternite of the prosoma; *f* ventral surface of the praegenital somite; *g* sternite of the genital somite (first opisthosomatic somite). *B* dorsal view, I to VI, prosomatic appendages; 1 *opisth.*, genital somite (first opisthosomatic somite). *C* lateral view. I to VI prosomatic appendages; *a*, *b*, *c* the three tergal plates of the prosoma; *praegen.*, the praegenital somite; 1 to 10, the ten somites of the opisthosoma. *D* chelicera. (Original drawing by Pocock and Pickard-Cambridge, after Hansen and Sørensen.)

* Grassi, *Natural. Sicil.*, iv, 1885, p. 127, and *Bull. Soc. ent. Ital.*, 1886, xviii, p. 153. Thorell, *Ann. Mus. Genova*, 1888, xxvi, p. 358; and Hansen and Sørensen, *Ent. Tidskr.*, 1897, xviii, p. 223. Augusta Rucker, *Q. J. Mic. Sci.*, xlvii, 1904, p. 215. Also *Zool. Jahrb. Morph.*, 1903 and *Amer. Nat.*, xxxv, 1901, p. 615; and Wheeler, *Amer. Nat.*, 1900, p. 837. C. Börner, *Zool. Anz.*, xxiv, 1901, p. 537. Hansen, *Ent. Tidskr.*, 1901, p. 193.

and the first and second pair of legs, and of two free segments, those of the third and fourth pair of legs (Fig. 545 *C*, *a*, *b*, *c*). According to Wheeler there are eleven abdominal segments; the first is small and forms the wasp-like waist, and the last three, the 9th, 10th and 11th (Fig. 545 *C*, 8, 9, 10) are also contracted. The last bears the post-anal multi-segmented flagelliform telson (comparable with that of *Thelyphonus*) with some fifteen joints, which probably have not the value of true segments.

The chelicerae are three-jointed and terminate in a scissor-like fang. The pedipalpi are nine-jointed; the first pair of legs is the longest and has twelve joints, the second and third have the more usual Arachnid number of seven joints, and the last has eight. The appendages do not appear to have any gnathobases; they arise well to the side of the ventral surface and their bases are separated by distinct sternal plates.

There are no eyes, but certain sensory organs occur on the cephalothorax and there are numerous hairs of systematic import. The crescentic mouth guarded in front by the epistome and behind by the hypostome opens into a chitin-lined pharynx. This passes into an oesophagus which pierces the chief nerve-mass and immediately enlarges into a sucking-stomach which is dilated by muscles running from it to the exoskeleton of the cephalothorax. This stomach opens by a valvular orifice into the intestine which gives off a pair of diverticula before leaving the cephalothorax. In the abdomen, the intestine enlarges and in the third to the seventh segments inclusive it gives off a pair of shallow diverticula. No malpighian tubules are present and no salivary glands. The intestine opens into a rectum which terminates in an anus. A pair of coxal glands occur in the cephalothorax and are said to open in front of the third pair of legs.

In *Prokoenenia* three pair of lung-sacs have been described, one on the fourth, one on the fifth and one on the sixth abdominal segments, but the evidence that they are more respiratory in function than the protrusible and retractile vesicles in the *Collembola* is yet to seek. No definite heart has yet been described.

The nerve-ganglia are highly concentrated; the supra-oesophageal and sub-oesophageal ganglia are fused into a large mass

pierced by the oesophagus. The supra-oesophageal ganglion, which is very large, supplies nerves to the median and lateral sense organs and to the chelicerae; the sub-oesophageal shows swellings corresponding with the remaining five pair of appendages, and it is connected with a single abdominal ganglion lying in the second and third segment of that region. The ovary is unpaired. It is prolonged anteriorly into two oviducts which swell out and fuse in the second abdominal segment; the vagina so constituted opens on the second abdominal segment. There is also a receptaculum seminis.

The primitively paired condition of the reproductive organs is retained in the testis. The paired tubular testes end anteriorly in much coiled vasa deferentia which enlarge to form vesiculae seminales. There are numerous accessory glands. The vasa deferentia open also on the ventral surface of the second abdominal segment. The spermatozoa are said to be immotile. Nothing is known of the embryology and but little of the young stages through which the animals pass before becoming adult. They occur under stones where a certain amount of moisture, which they seem to need, is usually retained.

There is but one family. Fam. **Koeneniidae**, with the characters of the Order. *Prokoenenia* with the so-called lung-sacs. *Prokoenenia wheeleri* from Texas and *P. chilensis* from Chili. *Eukoenenia* without the lung sacs; *Eukoenenia mirabilis*, Sicily, Italy, Tunis, *Eukoenenia siamensis* Siam; *E. augusta*, *E. florenciae* Texas, and *E. grassi* South America.

Order 5. **SOLIFUGAE (SOLPUGAE) ***

Cephalothorax (prosoma) covered by three fused segments followed by three free thoracic segments; the abdomen is not constricted and consists of ten segments; the chelicerae are chelate, the pedipalps leg-like; respiration tracheal; on the basal joint of the fourth legs are 3-5 racquet-shaped organs, the malleoli.

The segmentation of the Solifugae body approaches that of Insects inasmuch as there occurs a distinct head, thorax and

* Kraepelin, *Das Tierreich*, 12 Lff., Pedipalpi u. Solifugae, Berlin, 1901; and Bernard, *The Comparative Morphology of the Galeodidae*, *Tr. Lin. Soc.*, London, 2nd Ser., vi, 1894-97, p. 305.

abdomen. The head or cephalothorax consists of the segments bearing the chelicerae, the pedipalps and the first pair of walking legs, all fused to form a trapezoid-like mass bearing two dorsal simple eyes near the middle line. Ventrally there is no sternum, the coxae of the legs approximating. The mouth is borne on a rostrum which projects forward between the base of the powerful



FIG. 546.—*Galeodes araneoides*, Pallas. *a* Chelicerae; *b* eyes; *c* head; *d* thorax; *f* abdomen; *g* pedipalpi; *h* palpiform legs; *k* digital joint (capaule); *o* shear-like points of palps (end joint of chelicera); *r* anus.

chelicerae. A pair of thoracic stigmata lie between the coxae of the second and third legs. The abdomen consists of ten segments with sterna and terga and softer pleura connecting them. The first of these bears the genital pore, the second and third segments bear a pair of abdominal stigmata, and some species also have a median stigma on the fourth segment. The tenth segment bears the anus. There is little constriction between the abdomen and thorax.

The chelicerae are very large and powerful and by their shearing action the Solifugae can kill small mammals and birds, but as a rule they seem to live on insects. They bear a series of stridulating ridges and in the male a process termed the flagellum. The arrangement and size of the teeth on the claws is of value in classification. The pedipalpi are six-jointed and leg-like; they end in an eversible sense-organ, probably olfactory. The number of joints in the legs varies. The basal joints of the last pair of legs in the adult bears five racquet-shaped projections of doubtful function, the *malleoli*; probably they are sensory.

The Solifugae are animals of fair size, the smallest measuring from the tip of the chelicerae to the end of the abdomen 1.5 cm., the largest some 7 cm.

The mouth is situated at the end of the rostrum and is protected by certain bristles which aid in conducting the fluid food to the orifice. It opens into an oesophagus which traverses the beak and pierces the nerve ganglion. This is triradiate in section and can be expanded by the contraction of certain muscles, and thus it forms a sucking apparatus. There are no salivary glands. The oesophagus which is slightly coiled opens into the mid-gut which runs straight back to the hind-gut. The mid-gut has four pairs of the characteristic Arachnid pouches in the cephalothorax and thorax ; the anterior two pairs are small, but the third and fourth pairs penetrate into the ambulatory limbs. The abdominal pouches, sometimes called the "liver," are serially homologous with those in front and occupy a very large space in the abdomen ; they open into two lateral diverticula which communicate with the mid-gut. A pair of malpighian tubules open into the same region of the alimentary canal in the fourth abdominal segment. The hind-gut, which is lined by chitin, bears dorsally a stercoral pocket as in spiders.

The heart is a long tube, extending from the fourth or fifth segment to the thirteenth, it has two pair of thoracic and six pair of abdominal ostia. Anteriorly it ends in an aorta which seems to discharge the blood on to the central nerve ganglion. Posteriorly it commences as a vein.

The respiration is tracheal. The position of the stigmata is set forth above. The tracheae arising from one stigma communicate with those from the others.

A pair of coxal glands form coiled masses behind the nerve ganglion and open to the exterior between the coxae of the third and fourth walking legs.

In spite of the fact that in *Galeodes* the thoracic and abdominal segments remain free, the nervous system is highly concentrated. The supra-oesophageal ganglion supplies the chelicerae and eyes, the sub-oesophageal sends nerves to the pedipalpi and following appendages and other organs. Three nerves enter the abdomen from the hinder border of this ganglion ; the median of the three develops an abdominal ganglion ; this in the main supplies the intestine, whilst the lateral nerves pass to the generative organs.

A small endosternite lies under the mid-gut just behind the nerve mass, and a diaphragm, which is pierced by the heart,

alimentary canal, tracheae and nerves, separates the abdomen from the thorax.

Two ovarian tubules run one on either side of the abdomen. They do not form a ring as is so often the case in Arachnids, but they end blindly behind; anteriorly each enters a chitin-lined oviduct which ultimately fuses with its mate and opens to the exterior on the first abdominal segment. Four testicular tubules, two on each side of the alimentary canal, have been described, but our knowledge of the male is less complete than that of the female. There are no external organs of reproduction, and the male can only be told by the presence of the flagellum on the chelicerae or by some other minute secondary sexual character. The young undergo a considerable portion of their development within the ovary.

The majority of the Solifugae are nocturnal in their habits, though some species love the sunshine. Most, but not all, are active and run busily about making a hissing noise with their stridulators. There is much discrepancy in the accounts of the poisonous nature of their bites, but at any rate no poison gland has yet been discovered. They are for the most part very hairy. They are common in the warmer regions of the world, though they do not occur in Australia or in Madagascar. In Europe they are found in Spain, Greece, and in Southern Russia.

There are some twenty-four genera and a hundred-and-seventy species grouped in three families.

Fam. 1. **Galeodidae.** (Fig. 546.) The stigmata on 2nd and 3rd abdominal segments covered with a finely toothed plate. Only two eye-bristles. Flagellum lancet-shaped. The claws on the legs are hairy and there are claws on the 4th pair. *Galeodes* C. L. Koch, with 9 true species extends from N. Africa through Arabia, Syria, Armenia, S. Russia, Transcaucasia through Asia to further India. *Paragaleodes* Krpln. with six certain species extends from Morocco across N. Africa to Palestine, Syria, Arabia and Turkestan.

Fam. 2. **Solpugidae.** No tooth plate covering stigmata. Claws smooth. Two or many eye-bristles. Flagellum varies greatly.

Sub-fam. 1. **Rhagodinae.** *Rhagodes* with 22 species, Africa to S. of the Equator and Asia; *Dinorhax* with 1 species, *D. rostrum-psittaci*, Moluccas, Cochin China and Assam.

Sub-fam. 2. **Solpuginae.** *Solpuga* with 47 species extends all over Africa, *Zeriassa* with 3 species is found in S. and E. Africa.

Sub-fam. 3. **Daesiinae.** *Daesia* with 15 species extends throughout Africa, Palestine, Arabia and Cyprus; *Gnosippus*, 2 species found in Egypt and Palestine; *Blossia* 2 African species; *Gluvia* 1 species

in Spain ; *Hemiblossia* 1 species in S. Africa ; *Gluviopsis* 2 species in the Old World ; *Saronomus* 1 species from Venezuela ; *Procleobis* and *Pseudocleobis* have each one species from S. America ; *Ammotrecha* with 7 New World species ; *Mummucia* 1 S. American species.

Sub-fam. 4. **Eremobatinae**, *Eremobates* the single genus has 18 N. American species.

Sub-fam. 5. **Karschiinae**. *Ceroma* with 6 species extends from British East Africa to the Cape ; *Gylippus* 4 species Syria, Persia and Central Asia ; *Barrus* 1 Egyptian species ; *Eusimonia* 5 species North Africa to Central Asia ; *Karshia* 4 species Transcaucasia to Central Asia.

Fam. 3. **Hexisopodidae**. The 4th leg has no claws, some of the segments of the limbs spinous ; the tarsi of all the legs is one-jointed, no toothed plate over stigmata, flagellum filiform. This family contains but one genus *Hexisopus* with five species all confined to South Africa.

Order 6. **CHERNETIDIA (PSEUDO-SCORPIONIDA).***

Small tracheate Arachnida with chelate chelicerae and pedipalps ; abdomen segmented, without waist, with two pairs of stigmata and spinning organs ; postanal tail absent ; no eyes or 2 or 4 simple ones.

The Chernetidia (Figs. 547, 548) are small neat-looking Arachnids ; a quarter of an inch in length is their outside limit and as a rule they do not surpass an eighth. They are uniformly coloured as a rule and are mostly brown or chestnut.

The cephalothorax (prosoma) has either no traces of segmentation or at most one or two transverse striae. The two or four eyes—when eyes are present—are placed near the lateral edge. The abdomen (opisthosoma) has twelve segments with eleven terga, the last two being fused, and nine sterna, the last four being fused ; the terga may be in right or left halves separated from each other in the middle line by a membranous skin. The abdomen is capable of considerable extension, especially when the



FIG. 547.—*Obisium trombidioides*.
Kt Pedipalp.

* Bernard, *J. Lin. Soc.*, London, xxiv, 1894, p. 410. *Tr. Lin. Soc.*, London, Ser. ii, vi, 1894-7, p. 305. Croneberg, *Bull. Soc. Moscow*, Année 1888, 1899, p. 416. Pickard-Cambridge, *Monograph of the British Species of Chernetideae*, 1892.

eggs are maturing. There is no post-anal tail or spine of any kind.

The chelicerae are small and chelate, the movable joint of the chelae being pierced by the orifice of the duct of the spinning glands (*see* below). The chelicerae in certain families also bear a small toothed organ called the "galea," and in all the members of the group they bear a comb-like ridge, the "serrula," and a process, like the antenna of a Lamellicorn, termed the "flagellum." All these structures probably have something to do with the silk-spinning. The large pedipalps recall those of the scorpions and probably explain the second name of the group. They have six joints and are chelate, and their bases are produced in towards the mouth. The legs are slender and consist of from five to eight joints terminating in two claws, between which is a sucker like a pulvillus.

The generative pore lies on the first abdominal sternum which is also pierced by the ducts of certain abdominal glands. The stigmata lie, a pair behind the first, and a pair behind the second abdominal sternum, rather to the side.

The alimentary canal consists of a sucking-pharynx followed by a short oesophagus which traverses the chief nerve ganglion; the stomach gives off an unpaired diverticulum which passes ventrally and two lateral lobed diverticula which occupy a large part of the body; it then passes into a coiled or looped intestine, a very unusual feature in an Arachnid. The stercoral pocket is small and no malpighian tubules are known.

The tracheae of the first pair of stigmata pass forward and those of the second pair backwards. Rudimentary stigmata are described on the third and remaining segments of the abdomen.

A pair of coxal glands are well developed; they are U-shaped and internally the closed end consists of a syncytium of cells. They open on the coxae of the third pair of ambulatory limbs.

A pair of spinning glands lie in the cephalothorax and open to the exterior on the movable joint of the chelicerae. There are also large glands in the abdomen which open by two median papillae, one under the genital operculum and one on the anterior edge of the third abdominal segment; they probably produce a secretion which keeps the eggs together.

The heart consists of a dorsally placed tube, the number of ostia which open into it is still a matter of dispute; possibly it varies in different species.

The nervous system in the young is discrete, as many as sixteen ganglia being distinct, but in the adult these have fused into a common mass.

The ovary is median and has projections which contain the maturing ova. Laterally and anteriorly it is continuous with the right and left oviducts which form the typical arachnid ring uniting ventrally at the genital orifice. The testes form a network arrangement (a development of the ring), which communicates with a right and left vas deferens. A pair of accessory glands discharge their contents close to the external orifice. Two peculiar eversible structures are found in this region in the male. They are termed "ram's horns" and are by some authorities thought to have to do with the copulation. The eggs are carried about by the mother attached by some secretion to the ventral surface of the abdomen. The silk glands produce the silk for a web or nest in which the female retreats whilst the eggs mature.

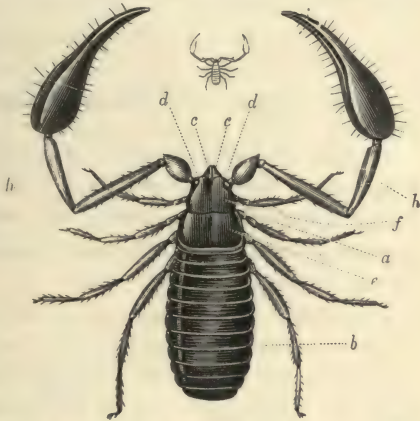


FIG. 548.—*Chelifer sesamoides*, Savigny. *a* Thorax (prosoma); *b* abdomen; *c* chelicerae; *d* eyes; *e* hinder segment of thorax; *f* front segment of thorax; *g* *h* pedipalpi.

The Chernetidia are carnivorous, feeding mainly on small insects or unresisting larvae. They are retiring in disposition and live for the most part under leaves, stones, bark and moss. They can as a rule run swiftly forwards, backwards, and sideways, and usually wave their large pedipalps in the air. Although seldom seen they are widely distributed, and this may partly be due to their habit of clinging with their pedipalps to flies and locusts and other insects which transport them in their flight. Various extant forms, such as *Chelifer* and *Chernes* are found in the Oligocene amber.

There is but one family—

Fam. 1. **Cheliferidae** with the characters of the Order. This includes 3 sub-families and 9 genera.

Sub-fam. 1. **Cheliferinae**. A galea and no epistome, eyes 2 or none. Two genera *Chelifer* (Fig. 548) and *Chernes*; *Chel. cancroides* is found in houses and sometimes termed the book-scorpion; *Chel. hermanni*, *Chel. cancroides*, *Chel. meridianus*, *Chel. subruber*, and *Chel. latreillii* are British. *Chernes* is blind, whilst *Chelifer* has two eyes. *Cher. nodosus*, *Cher. insuetus*, *Cher. cimicoides*, *Cher. dubius*, *Cher. phalaratus* are all British. Sub-fam. 2. **Garypinae**. The cephalothorax is contracted anteriorly, with 3 genera: *Chiridium muscorum* is British and like *Chel. cancroides* lives in houses, *Olpium*, *Garypus*. Sub-fam. 3. **Obisiinae**. Cephalothorax broad anteriorly, very large chelicerae. *Obisium* (Fig. 547) of which the species *O. muscorum*, *O. sylvaticum* and *O. maritimum* are British; *Roncus* with the British species *R. cambridgii* and *R. lubricus*; and *Chthonius* with *Chth. orthodatylos*, *Chth. rayi*, *Chth. tetrachelatus* and *Chth. tenuis* found in Great Britain.

Order 7. **PODOGONA (MERIDOGASTRA).**

Tergum of cephalothorax in two parts, the anterior hinged and hanging over the base of chelicerae; no cephalothoracic sternal plates visible; abdomen apparently of four segments; fifth pair of appendages modified in the male as intromittent organ; spiracles on the cephalothorax.

This order has recently been established* for the reception of the genera *Cryptostemma* and *Cryptocellus*. The squarish tergum of the cephalothorax is divided into an anterior hinged part, the "cucullus" which overhangs the mouth, and a larger posterior portion. The sternum requires dissection to make it evident. The abdomen consists of nine segments, but some of these are so small and so masked that only four segments are as a rule visible. The chelicerae are chelate and the pedipalps are weakly so. The coxae of the first three pair of legs are immovably fused, but those of the fourth and last pair are capable of restricted movement. The terminal joints of the third leg in the male are highly modified for depositing the semen. There are no eyes. The single pair of spiracles are situate on the cephalothorax above the coxae of the third legs. The genital aperture is between the second and third sterna of the abdomen.

* Lankester, *Q. J. M. Sci.*, xlviii, this contains a list of literature, but see also the very important memoir of Hansen and Sorensen *On Two Orders of Arachnida*, The University Press, Cambridge, 1904.

Fam. **Cryptostemmatidae.** The single family with the characters of the order contains two genera, *Cryptostemma* from West Africa and *Cryptocelis* from South America, the former with six species, the latter with two. The number of specimens which have been at the disposal of zoologists scarcely surpasses a score, and we know next to nothing of the inner anatomy, the habits or the development of these curious forms.

Order 8. PHALANGIDEA (OPILIONIDAE).*

Tracheate Arachnids with segmented abdomen which is united to the cephalothorax by its whole width, i.e. there is no waist ; there are as a rule no spinning glands ; two simple eyes ; chelicerae chelate but not the pedipalps which are not modified in the male ; the female lays egg and the young resemble their parents.

These creatures are usually known as “harvestmen.” They are of a fair size and are commonly mistaken for spiders, but the absence of waist and the segmentation of the abdomen serve to readily distinguish them.



FIG. 549.—*Phalangium opilio* ♂.

The cephalothorax bears on its dorsal surface an elevation or turret which is partially covered by spines and which bears laterally the two simple eyes. The abdomen is pushed forward on the ventral surface carrying on its anterior edge the generative pore ; a cephalothoracic sternum is present, but it is much reduced and masked by this projection of the anterior edge of

* Simon, *Arachnides de France*, vii, 1879. *Ann. Soc. Entom. Belg.*, xxii, 1879. Rössler, *Zeitschr. wiss. Zool.*, xxxvi, 1882. Sorensen, *Nat. Tidsskr.* (3), xiv, 1884. Thorell, *Ann. Mus. Genova*, viii, 1876. Pickard Cambridge, *Monograph of British Phalangids*.

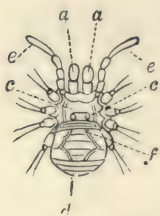


FIG. 550.—*Phalangium copticum*, Savigny. *a* Chelicerae; *e* eyes; *c* (to left) cephalothorax; *d* abdomen; *e* pedipalpi; *f* junctional line of thorax and abdomen.

the abdomen, and by the gnathobases of the pedipalps and of the anterior one or two pair of walking legs. The anterior segments of the abdomen have fused with the cephalothorax, but posteriorly at least three segments remain free (Fig. 550). The genital opening which is circular or transversely elongate is carried forward on the first abdominal segment, the two stigmata opening on each side of it possibly belonging to the second abdominal sternum. The chelicerae (Fig. 552) are toothed and chelate, the movable joint being the third.

The pedipalpi are longer with six joints; they may be clawed but are never chelate; the basal joint forms a gnathobase and is directed inwards towards the mouth.



FIG. 551.—A Phalangid or Harvestman, *Oligolophus spinosus*, adult male $\times 2$. 1 chelicerae; 2 pedipalps; 3, 4, 5 and 6 first, second, third, and fourth legs.

The legs of the Phalangidea form one of their characteristic features; they are as in the Araneida seven-jointed, but the joints except the area which is fused with the cephalothorax are often much elongated and the legs are very long and brittle. The tarsi are multiarticulate and terminate in one or two claws. The first and in many cases the second legs bear gnathobases.



FIG. 552.—Chelicerae and pedipalpi of *Phalangium copticum*, seen from in front.

There is a thin-walled pharynx with teeth within the mouth, and just behind it; traversing the nerve-mass is a moderately fine oesophagus which dilates posteriorly and then enlarges into a spacious stomach + intestine which passes straight to the anus. This stomach + intestine bears (some thirty) caeca of varying sizes, usually paired; these however remain distinct and do not become entangled together to form a gland like the so-called liver of the Araneida. The anus is terminal. Phalangids, unlike spiders, eat solid food which may be triturated by the gnathobases and by the pharyngeal teeth.

The heart is a dorsal tube with three chambers and three pair of ostia; little more is as yet known about the circulatory system. The tracheae provide a complex system strengthened by spiral thickenings; the stigmata lead at first into large spacious chambers from which the fine tracheae are given off.

A pair of malpighian tubules open into the intestine, and a pair of coiled coxal glands, bearing internally a well-marked vesicle, open on the base of the third ambulatory leg. There are no spinning glands except in the Cyphophthalmi.

The supra-oesophageal ganglion gives off nerves to the eyes and to the chelicerae. It is a somewhat pyramidal-shaped nerve-mass and it passes laterally into the star-shaped composite ventral ganglion which gives off nerves to the other appendages. Posteriorly it gives off a median and two lateral nerves which branch and bear ganglia and supply the structures in the abdomen. There is a stomatogastric system of nerves.

Both sexes have long protrusible organs for emitting the products of the gonads (Fig. 552 *bis*). The ovipositor and the penis are usually retracted; when extended they are almost as long as the body. Both ovary and testis are annular and the former is papillated with the maturing ova. There is a spacious

uterus and accessory glands. The eggs are actually fertilized within the ovary. The ends of the annular testis fuse and form a coiled vas deferens which expands into a vesicula

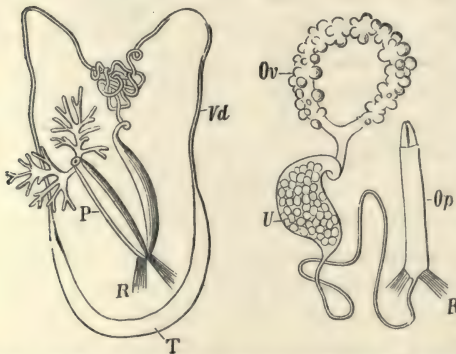


FIG. 552 bis.—Male and female generative organs of *Phalangium opilio* (after Krohn). *T* testis; *Vd* vasa deferentia; *P* penis with accessory glands; *R* retractor muscles; *Ov* ovary; *U* uterus; *Op* ovipositor.

seminis just before it enters the penis. It is by no means rare to find ova abnormally occurring in the testis of a Phalangid.

Except when in use the penis and the ovipositor are not visible, and then in the genera *Trogulus* and *Siro* it is not possible to determine the sex. In other Phalangids however the male is small

and more vividly coloured than the female. At the time of reproduction the males indulge in “combats acharnés.”* The eggs are laid in the earth and under stones, leaves, etc., during the autumn and hatch out the following spring. As autumn comes on the adults gradually die and with some exceptions, i.e. the Trogulidae and Nemastomatidae which live for some years, they do not survive the winter except in the form of eggs. They are hatched out as miniature Phalangids but white in colour.

The adults have no organs of defence unless the evil-smelling secretion, which exudes in some species from two pores close to the anterior coxae, be counted as such. Their safety lies in their power of flight or of shamming death. Their long legs are well adapted for running on grass or stubble, but are easily broken. They are a thirsty race and have often been observed drinking the dew and sucking vegetable juices.

The Phalangids are cosmopolitan and are found in all latitudes. Of the three primary groups the Cyphophthalmi are temperate and tropical, the Mecostethi are proper to the warmer regions of the world, whilst the Plagiostethi are temperate in their distribution.

* Simon.

Sub-order 1. **CYPHOPHTHALMI.**

First sternal plate of abdomen small and leaving genital orifice exposed. Ten tergal and nine sternal plates in abdomen. 2 or 4 marginal eyes on pedicels; the anterior abdominal segment does not extend in front of the coxae of last legs; sternum of prosoma long and narrow; two or four stigmata.

Fam. 1. **Sironidae.** Sternum long and very narrow, two eyes and two stigmata. *Siro* with two species, France and Corsica; *Cyphophthalmus* southern Europe; *Stylocellus* Sumatra and *Petrallus* Ceylon.

(Fam. 2. **Gibocellidae**, with 4 eyes and 4 stigmata, are represented by a single species *Gibocellum sudeticum* from Bohemia. There is some doubt if this animal really exists.)

Sub-order 2. **MEGOSTETHI.**

The three last segments of the abdomen remain free; the coxae of the posterior legs are fused with the first abdominal sternum, but the remaining abdominal sterna are free; eyes usually borne on a frontal ridge; sternum of prosoma long and narrow; the anterior four legs bear one claw, the posterior four two claws each.



FIG. 553.—*Phalangium copticum* Sav. Natural size and magnified.

Fam. 1. **Phalangodidae.** Body wedge-shaped, broadest behind; the posterior abdominal sternum is the largest; sternum of prosoma almost linear; coxae all immovable; stigmata concealed. This family

belongs with some exceptions to the hotter regions of the Old World. *Phalangodes*, the European species, has also North American and Australian representatives. *Mermerus*, *Epidanus*, *Maracaudus* and *Sitalces* are tropical genera.

Fam. 2. **Gonyleptidae**, this family is distinguished from the preceding by the absence of a longitudinal stripe on the cephalothorax. They are exclusively American, *Gonyleptus*.

Fam. 3. **Cosmetidae**, also from America.

Sub-order 3. PLAGIOSTETHI.

The last three segments are free or their segmentation is indicated by striae; the anterior abdominal sternum is pushed forward as far as the first pair of coxae; prosomatic sternum very short; a single claw on all the legs. Mostly denizens of temperate regions.

Fam. 1. **Phalangiidae**. Integument soft or coriaceous; two eyes on an eminence well removed from border of cephalothorax; the 2nd pair of legs have well-marked gnathobases; the tarsus of the pedipalps is much longer than the tibia and ends in a claw. *Sclerosoma* with 2 British species; *Mastobunus*; *Astroburnus*; *Liobunum* with 2 British species has very small body and very long legs; *Prosalpia* a high mountain form; *Phalangium* (Figs. 549, 550) the form commonly seen on walls, has 4 British species; *Dasylobus*, *Platybunus*, with 2 British species; *Megabunus* with 1 species found in our islands; *Gigas* the largest member of the family, *Oligolophus* (Fig. 551) has 8 British species; *Acantholophus* as its name indicates is a spiny form.

Fam. 2. **Ischyropsalidae**. Coriaceous, with a longitudinal stripe; two eyes on an eminence removed from the border of the cephalothorax; coxae free; gnathobases of 2nd legs reduced to tubercles; pedipalps long with no claw, their tarsus is shorter than the two preceding joints. *Sabacon* lives in caves and grottoes; *Ischyropsalis* in the same localities and in moss.

Fam. 3. **Nemastomatidae**. Coriaceous, no stripe on cephalothorax; 2 eyes on an eminence near the anterior border of the cephalothorax; coxae free; pedipalps as in preceding family; no gnathobase on 2nd pair of legs. The single genus *Nemastoma* has 2 British representatives, they live in moss and the damp débris of forests.

Fam. 4. **Trogulidae**. Very hard, firm exoskeleton; cephalothorax produced in a bifurcated hood with overhangs mouth; coxae fused to cephalothoracic sterna; no gnathobase on 2nd pair of legs; pedipalps moderate or short; their tarsi and claws as in preceding two families. They are rather mite-like Phalangids with deliberate movements. *Dicranolasma*, *Anelasmoecephalus* with 1 British species; *Calathocratus*; *Trogulus* with 1 British species; *Metopoctea*.

Order 9. ACARINA (Mites).*

Degenerate Arachnids allied to the Phalangids. The abdomen is usually unsegmented and broadly fused with the thorax. The

* O. Fr. Müller, "Hydrachnae," etc., 1781. A. Dugès, "Recherches sur l'ordre des Acariens en général et les familles des Trombidies, Hydra-

basal segments of the pedipalps are united behind the mouth, but those of the following segments are widely separated and have no gnathobases. Respiratory stigmata, when present, are usually cephalothoracic.

The mites are divided up in a very large number of species, not perhaps so many as are the spiders, but into far more than any other Arachnid group. They also at times show a most

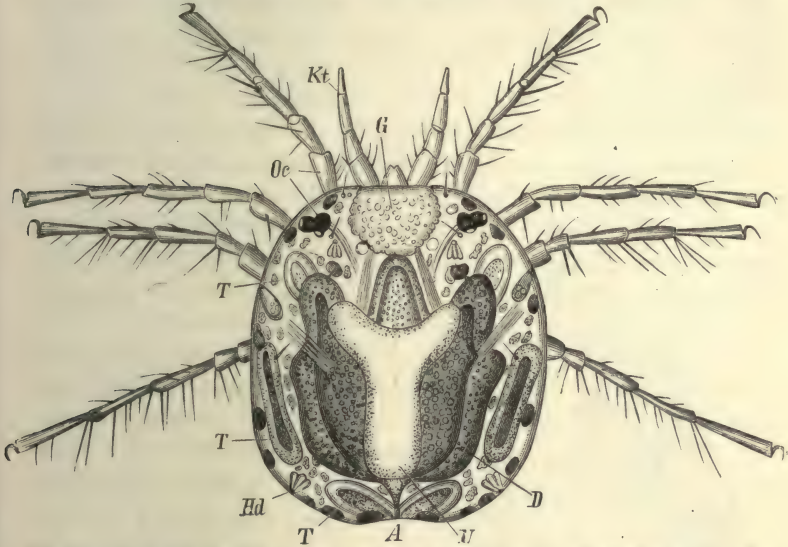


FIG. 554.—Ripe male of *Atax Bonzi*, seen from the dorsal surface (after E. Claparède). *Kt* Pedipalpus; *G* brain; *Oc* eyes; *T* testis; *N* Y-shaped gland; *D* intestine; *A* anus; *Hd* cutaneous glands.

rapid rate of reproduction and hence if conditions are favourable very large numbers of individuals are met with.

They are for the most part minute, except the ticks, which swell visibly after a meal of blood. Mites seldom surpass a millimetre in length, whilst many are microscopic.

chnés en part," *Ann. des Sc. Nat.*, ii. Ser., Tom. i. and ii. H. Nicolet, "Histoire naturelle des Acariens, etc. Oribatides," *Archives du Musée d'hist. Nat.*, Tom. vii. O. Fürstenberg, "Die Krätzmilben des Menschen und der Thiere," Leipzig, 1861. Al. Pagenstecher, "Beiträge zur Anatomie der Milben," i. and ii., Leipzig, 1860–1861. E. Claparède, "Studien an Acariden," *Zeitschr. für wiss. Zool.*, Tom. xviii., 1868. P. Mégnin, "Les parasites et les maladies parasitaires," 1880. A. D. Michael, "Oribatidae" *Das Tierreich* Lief. iii. A. Nalepa, "Eriophyidae (Phytoptidae)," *op. cit.* Lief. iv. G. Canestrini, and P. Kramer, "Demodicidae und Sarcop-
tidae," *op. cit.* Lief. vii. R. Piersig, und H. Lohmann, "Hvdrachnidae und Halacaridae," *op. cit.* Lief. xiii.

Many of them live parasitically on both plants and animals or on decaying organic matter. They vary greatly in shape, some being elongated, but perhaps their commonest form is a rounded oval more or less arched dorsally and flattened on the ventral surface (Fig. 554). The abdomen is as a rule separated from the cephalothorax by a line or by a shallow groove, never by a deep constriction. The anterior segments may be separated off from the rest of the cephalothorax and when this is the case they constitute the "capitulum." Many mites are blind but many have numerous eyes. The number of these however varies capriciously and is little used in classification. The cuticle is usually soft, but is hard and thick in the Oribatidae. It bears numerous hairs and markings and is sometimes highly coloured.

The chelicerae may be chelate with the movable claw ventral to the fixed. Frequently, however, they are much modified, and in some groups they are reduced to piercing stylets with or without serrated edges. The pedipalps, which comprise

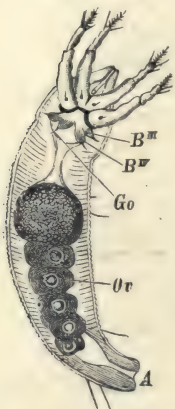


FIG. 555.—Female of *Eriophyes vitis*, from the leaf of the vine (after H. Landols). *Ov* Ovaries; *A* anus; *Go* genital opening; *BIII*, *BIV* third and fourth pair of legs.

more than five joints, are subject to great diversity of form but are usually leg-like, sometimes ending in a raptorial claw capable of holding prey; occasionally they become almost antenniform. Their basal joints unite in the middle ventral line behind the mouth, constituting the so-called labium. Except the Eriophyidae (Phytoptidae) which have but two pairs of legs, (Fig. 555) mites have the usual Arachnid arrangement, viz. four pairs. The legs are six- or seven-jointed as a rule, though there is much variation on this point, and they may end in claws (1–3), suckers or hairs or some combination of these organs. The claws are often beautifully adapted to the needs of the animal, fitting for instance exactly round the

hairs of the mammal on which the mite is living. The abdomen may be rounded or elongate (*Demodex*) and it is then sometimes ringed (Fig. 567).

The mouth is usually small and it leads, at any rate in some species, into a sucking pharynx, whence arises a fine oesophagus

which pierces the concentrated nerve ganglion and then dilates into a globular stomach. Salivary glands are conspicuous in some of the ticks (Fig. 556). The intestine gives off a comparatively small number of caeca, two of which are large and pass backward (Fig. 556 *D*). In some cases, as in spiders, the caeca are continued into the coxae of the legs. The intestine may be divided into a small intestine and colon and rectum, and in any case the malpighian tubules arise between the last named regions. No connexion has yet been found between the stomach and the rectum in certain of the Trombidiidae. In this family the former ends blindly and the latter is a simple sac packed apparently with excretory products. In some genera paired coxal glands supplement the malpighian tubules.

Many years ago a two-chambered heart was described in certain of the Gamasidae, but since that time no one has succeeded in seeing it and it seems probable that there is no specialized organ for propelling the blood in mites and that the circulation is lacunar and promoted by the movement of muscles and certain rhythmic pulsations of the alimentary canal.

The respiratory organs are tracheae, often long and convoluted. In aquatic species they are often absent. The stigmata are either paired and open near the base of the chelicerae, or above and behind the base of the 4th, 5th or 6th appendages, or in the articular sockets of these or of the 3rd pair, or finally they are united and open on the dorsal surface. This diversity of position is used in classification.

The nervous system is very concentrated; an oval mass with little indication of its component parts is pierced by the oesophagus. From it radiate many nerves, but there is no dominant

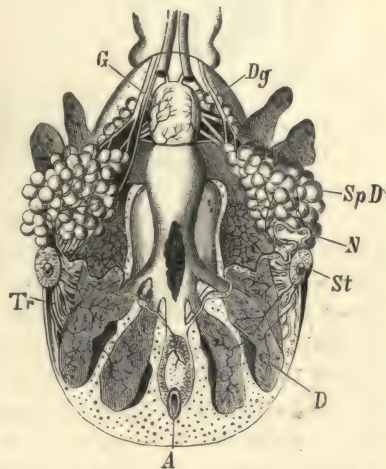


FIG. 556.—Anatomy of *Ixodes ricinus* (after Al. Pagenstecher). *G* Brain; *SpD* salivary gland; *Dg* ducts of salivary gland; *D* diverticula of intestine; *A* anus; *N* malpighian tube; *Tr* bundles of tracheae; *St* stigma.

ventral nerve cord. The sense organs are eyes but these are not always present. Sensory hairs also exist and with these may be grouped the pseudostigmatic organs of the Oribatidae which protrude from sockets on the dorsal side of the cephalothorax.

The reproductive organs (Fig. 557) are typically annular and much alike in both sexes. The two testes are fused, and each opens

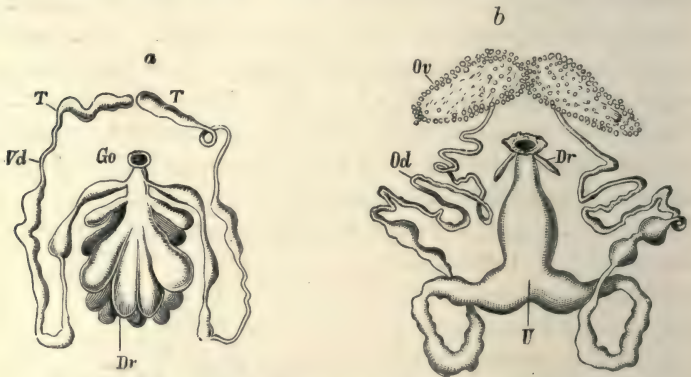


FIG. 557.—*a* Male; *b* female genital organs of a Mite *Argas* (after Al. Pagenstecher). *T* Testes; *Vd* seminal duct; *Dr* prostate gland; *Go* genital opening; *Ov* ovaries; *Od* oviduct; *U* uterus; *Dr* glandular appendages.

into a vas deferens. These unite at the external opening which lies in the ventral middle line, usually between the last pair of legs, but it may be shifted even more anteriorly. The male often bears a pair of suckers near the posterior end of the body and in many genera there is an intromittent organ. In some cases where this is absent the chelicerae deposit the spermatophore at the genital opening of the female in something the same way as the pedipalpi do in spiders. The ovaries are fused and their oviducts unite into a uterus or vagina whose opening corresponds in position with that of the males. An ovipositor may be present.

Mites undergo a metamorphosis (Fig. 558) and pass through several instars before becoming adult, but the stages are not the same in all species. The first is the *egg* which is usually undeveloped at oviposition, but in some of the Oribatidae is almost ready for hatching. The second is the *deutovum* which occurs for instance in *Atax*; here an outer eggshell becomes hard and brown and then splits longitudinally, thus allowing for the growth of the larva whilst at the same time affording it some protection. The

third is the *larva*, which almost invariably has but three pairs of legs (Fig. 558). The fourth is the *nymph*, which lasts from the moult which leaves the larva with its complete complement of four pair of legs, until the last moult which produces the adult.

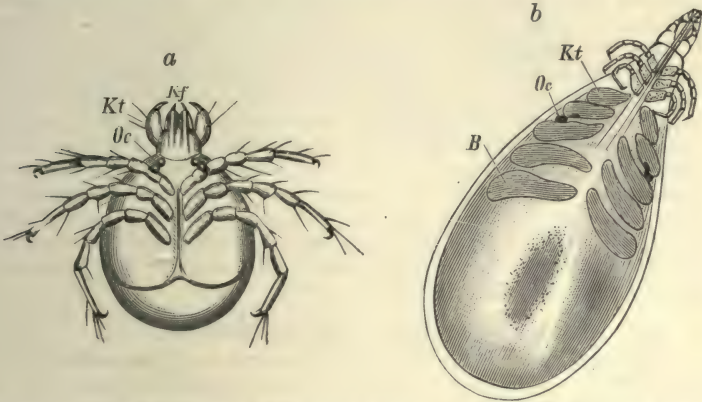


FIG. 558.—Larva of a *Hydrachna*. *b* Its pupa (nymph); *Kf* chelicera; *Kt* pedipalpus; *Oc* eyes; *B* legs.

The nymph is at first active, but this stage is succeeded by a longer or shorter period of rest during which the tissues are resolved and reconstituted as in a Dipterous insect. The fifth instar is the *adult* which often differs markedly from the nymph; so much is this the case in *Tyroglyphus*, the cheese mite, that the young nymphs were for long thought to belong to a different genus (*Hypopus*), and the stage is still referred to as the hypopial stage. During the hypopial stage the mite can resist comparative drought and by clinging on to insects, etc., effect the distribution of the members of the family.

We have taken our classification in the main from Lankester* who however does not differ very widely from Trouessart.† There are seven sub-orders and thirteen families of very varying extent.

Sub-order 1. NOTOSTIGMATA. ‡

Skeleton soft without sclerites, the abdomen has 10 segments, the anterior four of which each bear a single pair of stigmata.

Fam. 1. **Opilioacaridae (Eucaridae).** This family contains 1 genus

* *Q. J. Micr. Sci.*, xlviii, 1904, p. 165.

† *Rev. Sci. Nat. Quest.*, ii, 1892, p. 20.

‡ With, *Vid. Med. Copenhagen*, 1904, pp. 137–192.

Opilioacarus (*Eucarus*), in which the genital pore is pushed forward so as to lie between the coxae of the 3rd pair of legs; there are but 3 species, *O. segmentatus* from Algeria, *O. italicus* from Sicily and *O. arabicus* from Aden.

Sub-order 2. CRYPTOSTIGMATA.

Hard integument, with a continuous dorsal and ventral sclerite; the stigmata typically open at the base of all the legs, and are concealed in the socket or acetabulum. The cephalothorax bears pseudostigmatic organs; blind.

Fam. 2. **Oribatidae**.* Nonparasitic, vegetable-eating mites whose hard cuticle has earned them the name of "beetle" mites. Usually found under bark, amongst moss, or lichens and fungi or under stones. A few are aquatic. *Pelops* with 10 species; *Oribata* with 45 species; usually in moss, as are the two species of *Serrarius*; *Zetorchestes* 1 species; *Scutovertex*, *Cepheus*, *Tegeocranus* with 5 or 6 species each; *Carabodes* and *Liacarus* with 9 or 10 species; *Notaspis* with 26 species; *Amerus* with 1 species; *Damaeus* with 21 species; *Hermannia* with 9 species; *Neoliodes* and *Cymbaeremaeus* with 3 or 4 species; *Nothrus* with 19 species; *Lohmannia* with 2 species; *Hypochthonius* with 5 species; *Hoploclerema* with eight species; *Phthiracarus* with 7 species.

Sub-order 3. METASTIGMATA.

Integument mostly hard, tracheae opening by a pair of stigmata above and behind the base of the fourth or fifth or sixth pair of appendages. This sub-order includes the ticks.

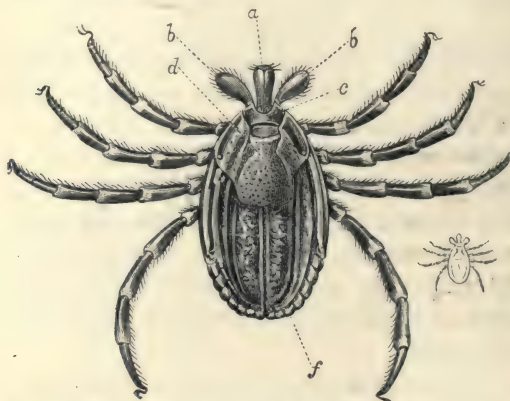


FIG. 559.—*Hyalomma aegyptium*, Savigny. a Chelicerae; b Pedipalpi; c head; d thorax; f abdomen.

Fam. 3. **Gamasidae**. Carnivorous mites, free on the ground or parasitic and then often on Insects, chelicerae chelate, pedipalps free, tarsi two-jointed with a caruncle or sucking disk, no eyes, 2nd pair of legs often stouter than the others. *Gamasus coleoptratorum* is often found attached to the beetle *Geotrupes*, *G. marginatus* lives on corpses; *Uropoda*,

this genus attaches itself to beetles by a thread formed of viscid excreta from the anus; *Dermanyssus* mostly parasitic on birds and bats, *D. avium* infests aviaries and poultry-yards; *Zercon*; *Pteroptus* lives on bats.

Fam. 4. **Argasidae**.† The rostrum is inferior and the mouth parts

* A. D. Michael, *British Oribatidae*, Ray Society, 1894, and *Das Tierreich*, 3 Lieferung, Oribatidae.

† Neumann, Revision de la famille des Ixodidés, *Mem. Soc. Zool. France*, viii, 1895; x, 1897; xii, 1899; xiv, 1901. Neumann classes the Argasidae as a sub-family, the Argasinae, which with the sub-family Ixodinae make up the family Ixodidae.

concealed from above, stigmata between the two last pair of legs, integument leathery and granulated; eyes may be present.

This and the next family are most formidable foes both to man and domesticated and feral animals. They convey a Protozoan parasite, which is as a rule a species of *Piroplasma*, from one host to another just as *Anopheles* conveys the malaria organism. Nothing is known as to what goes on in the body of the tick as the parasite cannot be found there; perhaps it breaks up into ultra-microscopic spores, but it is known that in the case of Texas fever an infected female tick can infect her eggs and that these give rise to infected larvae. The members of this family attack mammals and birds, especially the latter. *Argas* with 8 species (Fig. 551). *A. persicus* attacks man in Western Asia often with fatal results. *Ornithodoros* with 11 species has one European representative *O. talaje*. Like the Ixodidae the members of this family seem to flourish best in warm climates.

Fam. 5. **Ixodidae.*** The terminal rostrum comprises (1) a basal portion, (2) a pair of pedipalps, (3) a hypostome beset with recurved hooks,

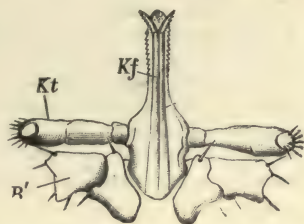


FIG. 560.—Oral apparatus of *Ixodes* (after Al. Pagenstecher). *Kf* chelicera; *Kt* pedipalpus; *R'* first pair of legs.

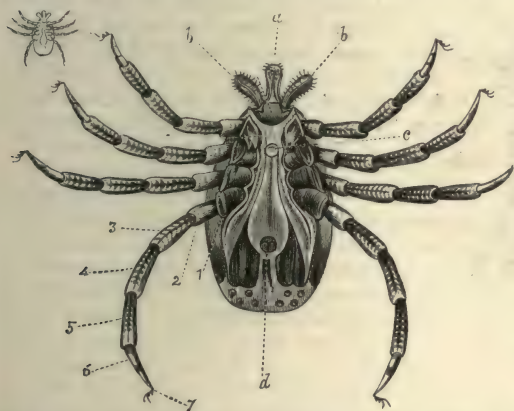


FIG. 561.—*Hyalomma aegyptium*, under side. *a* Chelicerae; *b* pedipalpi; *c* genital aperture; *d* anal aperture; 1-7 joints of leg.

and (4) a pair of chelicerae, cutting instruments with serrated outer border. The sucking tube is between the hypostome and chelicerae. Integument leathery, stigmata behind the coxae of the last legs, male very much smaller than the gorged female, the latter is when young flattened but the development of the eggs, aided by the sucking of blood, brings about an enormous increase

in size and the body may attain the size of a filbert. The males are enclosed in a dorsal shield which does not permit them to swell as the females do. The larvae of most ticks live upon and amongst plants, but they readily seize hold of passing animals and thrust their rostrum into the victim's skin. The Ixodidae are parasitic upon mammals and to a less degree on birds and reptiles, but the several species are catholic in their tastes and do not confine

* Neumann v. supra.

their attentions to one species of host. *Ixodes* (Figs. 560, 556) with some 30 species is capable of living in comparatively cold countries, this genus is blind, *I. ricinus* is the common dog tick; *Eschatocephalus* (*Haemalastor*) with 5 species; *Aponomma* with 14 species inhabits the warmer regions of the Old World and is often parasitic on snakes and other reptiles; *Amblyomma* with over 70 species requires a tropical climate and is largely American and African but it reaches Asia. *A. hebraeum* is the well-known "Bont-tick" of S. Africa; *Hyglomma* (Figs. 559, 561) 3 species largely African but it also extends into Asia; *Haemaphysalis* with 18 species is largely Asian; *Rhipicephalus* with 14 species is chiefly African, but spreads to Asia and Europe and has been widely distributed by man. *R. annulatus* conveys the parasite which causes the Texas or Red-Water fever in cattle, several species attack sheep; *Dermacentor* with 7 species.

Sub-order 4. PROSTIGMATA.

Stigmata, when present, lie close to or above the bases of the chelicerae: they are absent in some aquatic forms. Integument soft but with sclerites, those on the ventral surface apparently represent the proximal segment of the legs embedded in the body.

Fam. 6. **Trombididae.** The pedipalps usually have the 2nd joint longest and a finger and thumb arrangement at the tip, some live on plants and some are carnivorous, tarsi 2-clawed and without a caruncle. *Tetranychus telarius* the red "spider" of our hot-houses spins threads from a papilla near the



FIG. 562.—*Trombidium holosericeum* (after Mégnin).

end of the abdomen, many other species of this genus damage plants; *Rhaphignathus*, *Bryobia* with long anterior legs; *Trombidium holosericeum* (Fig. 562) is the commonest of the "harvest mites," in its youth it is parasitic on Phalangids; *Caeculus* mimics Phalangids; *Tarsonemus* attacks plants.

Fam. 7. **Hydrachnidae.*** Freshwater mites with legs provided with long, closely packed hairs adapted for swimming. Predaceous with the earlier stages often parasitic on water insects (Fig. 558). The Hydrachnidae are very widely distributed; they are mostly freshwater but some, such as many species of *Hydrachna* and of *Hydryphantes*, and others live in brackish water, whilst *Pontarachna* and *Nautarachna* have marine representatives. They live on other organisms, chiefly on species of *Daphnia* and *Cypris*, more seldom on *Cyclops*, Gnat-larvae and Infusoria. *Limnochares* 2 species lives in mud, *Eulais*, young stages parasitic on aerial insects, 35 species; *Piersigia*, *Diplodontus*, *Bargena*, *Thyopsis*, *Pseudothyas*, *Partnumia*, *Tanaognathus*, *Mamersa*, *Midea*, *Xystonotus*, *Mideopsis*, *Axonopsis*, *Albia*, *Brachypoda*, *Ljanina*, *Frontipoda*, *Gnaphiscus*, *Pseudosperchon*, *Limnesiopsis*, *Koenikea*, *Capobates*, *Tyrrellia*, *Wettina*, *Pionopsis*, *Ecpolus*, *Encentridophorus*, *Najadicola*, *Huitfeldtia*, *Nautarachna* and *Kongsbergia* are all

* Piersig and Lohmann, *Das Tierreich*, 13 Lieferung, Hydrachnidae and Halacaridae.

genera with but a single species; *Hydrachna* with 33 species, *Thyas* with 8 species, *Paniscus* with 4 species, *Protzia* with 2 species, *Eupatra* with 4 species, *Hydryphantus* with 17 species, *Krendowskia* with 3 species, *Arrhenurus* a very large genus with about 100 species, *Aturus* with 4 species, *Torrenticola* with 2 species, *Lebertia* with 6 species, *Oxus* with 8 species, *Teutonia* with 2 species, *Sperchon* with 14 species, *Limnesia* with 12 species, *Atractides* with 5 species, *Hygrobates* with 11 species, *Hydrochoreutes* with 3 species, *Pionacercus* with 4 species, *Laminipes* with 5 species, *Atax* with 27 species, the well-known *Atax bonzi* infests fresh-water mussels (Fig. 554); *Neumania* with 11 species, *Feltria* with 10 species, *Tiphys* with 9 species, *Piona* with 34 species and *Pontarachna* with 3 species.

Fam. 8. **Halacaridae**.* Marine, the head bearing the chelicerae and pedipalps (the capitulum) is movably articulated with the body, usually an anterior and a posterior dorsal, hard, sclerite, and two side ones protecting the eyes, legs attached to the side of the body. This is a comparatively small family of marine mites which do not swim but crawl about on sea-weed and hydroids, ascidians, etc. They are for the most part predaceous, but *Rhombognathus* eats sea-weeds. They are widely distributed both horizontally and vertically. *Halixodes*, *Atelopsalis*, *Acaromantis* have each one species, *Coloboceras*, *Scaptognathus* and *Simognathus* each two, *Trouessartella* three, *Agave* seven, and *Halacarus* 41 species.

Fam. 9. **Bdellidae**. These long-nosed or snouted mites are distinguished by the marked separation of their "capitulum" or "head" from the rest of the body, chelicerae chelate and long and projecting, pedipalps tactile and elbowed; usually bright in colour, often red; larvae attach themselves to spiders and beetles but the adults are free and predaceous. *Scirus*, *Bdella*, *Ammonia*, *Eupalus*, *Cheyletus* (Fig. 563) sometimes placed in a separate family, *Cryptognathus*, *Eupodes* and others.



FIG. 563.—*Cheyletus flabellifer* (Book Mite, quite unconnected with books).

Sub-order 5. ASTIGMATA.

* Degenerate, usually parasitic mites which approach the Prostigmata in the development of the integumental sclerites, soft skin, no tracheae.

Fam. 10. **Sarcoptidae**.† Rounded posterior end of the body; legs mostly 5-jointed with 1 or 2 claws; eyes seldom found; sexes usually markedly different. Most parasitic on or in the skin of Mammals, Birds and Insects. There are numerous sub-families. Sub-fam. 1. **Cytolichinae**, *Cytolichus* and *Laminosioptes* each with one species. Sub-fam. 2. **Sarco-**

* Piersig and Lohmann, *Das Tierreich*, 13 Lieferung, Hydrachnidae and Halacaridae.

† Canestrini and Kramer, Demodicidae and Sarcoptidae (including Tyroglyphidae) *Das Tierreich* 7th Lief. 1899.

ptinae the so-called Itch mites, *Notoedres*, *Prosopodectes*, *Sarcoptes*, *S. scabiei* (Fig. 564) attacks man, burrowing in the epidermis, *Cnemidocoptes*, *Psoroptes*, *Psoralgæ*, *Chorioptes* (Fig. 565), *Caparinia*, *Otodectes*. Sub-fam. 3. **Canestriniinae**, mostly parasitic on insects, *Linobia*, *Canestrinia*, *Coleopterophagus*. *Hemisarcoptes*. Sub-fam. 4. **Listrophorinae**, living amongst the hairs

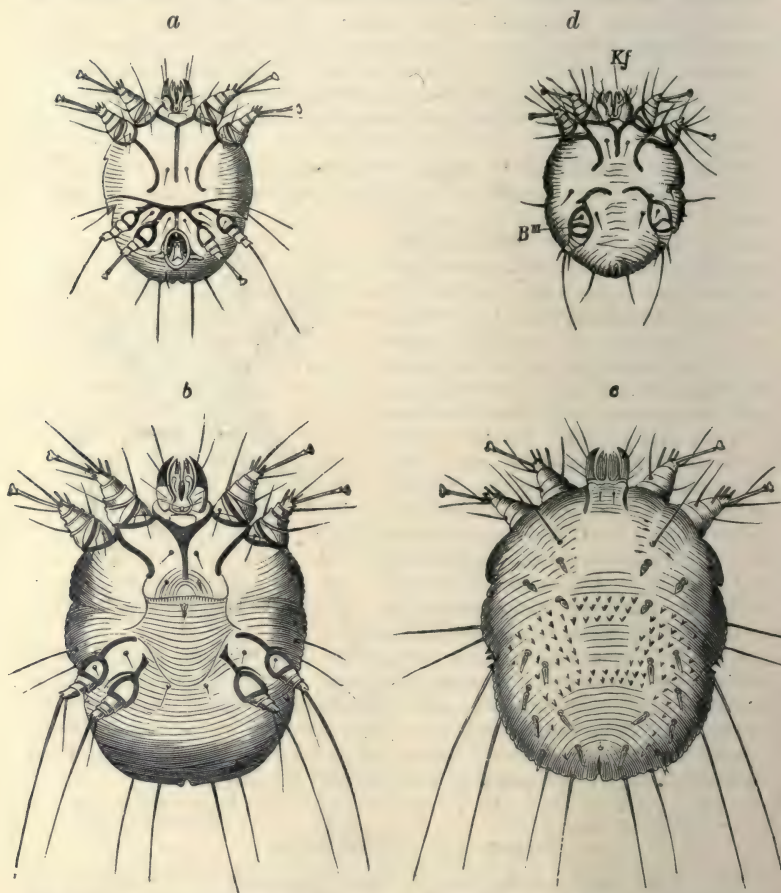


FIG. 564.—*Sarcoptes scabiei* (after Gudden). *a* Male from the ventral side; *b* female from the ventral side; *c* female from the dorsal surface; *d* larva; *Kf* Chelicerae; *B'''* third pair of legs.

of mammals, *Listrophorus*, *Myocoptes*, *Trichoeius*, *Schizocarpus*, *Campylorchirus*, *Labidocarpus*, *Chiroadiscus*. Sub-fam. 5. **Analginae**, these mites live in or on the feathers of birds and sometimes burrow in the skin. *Freyana*, *Pterolichus*, *Xoloptes*, *Falculifer*, *Chiloceras*, *Bdellorhynchus*, *Anasicydium*, *Thecarthra*, *Neumannia*, *Syringobia*, *Dermoglyphus*, *Sphaerogastra*, *Pteronyssus*, *Analges*, *Protalges*, *Mégninia*, *Nealges*, *Pteralloptes*, *Xolalges*, *Alloptes*, *Allanalges*, *Proctophyllodes*, *Trouessartia*, *Pterodectes*,

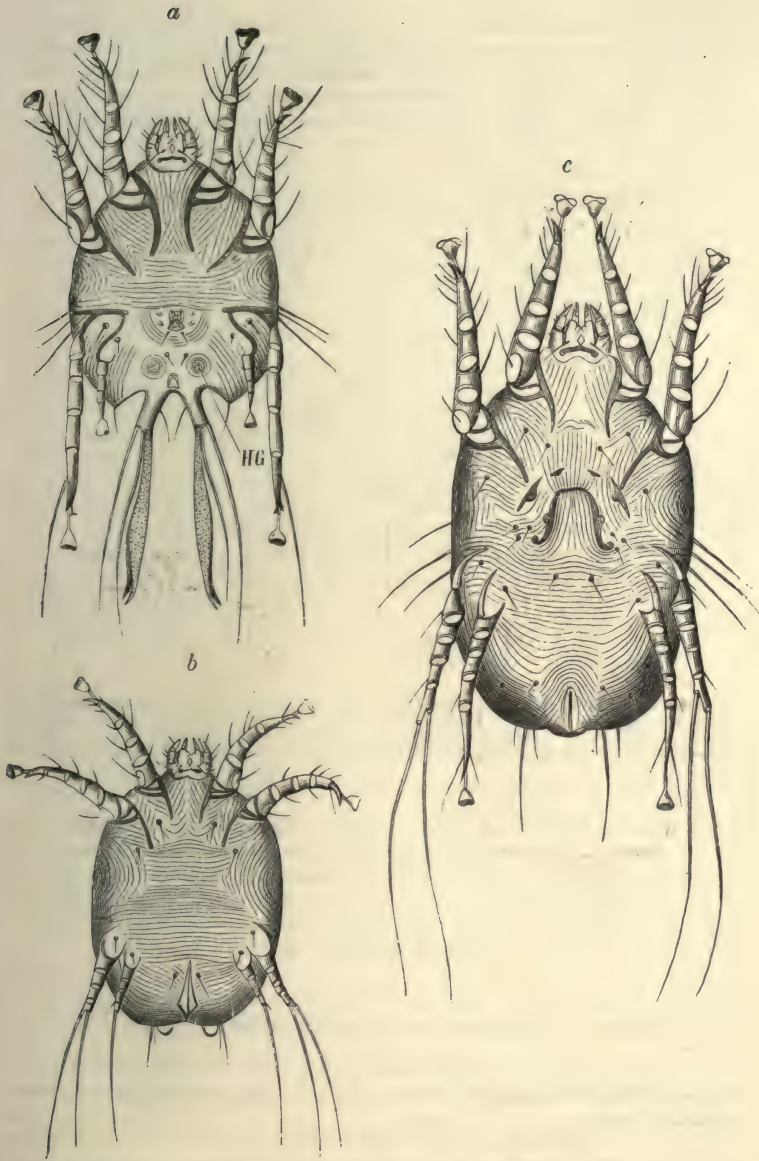


FIG. 565.—*Chorioptes spathiferus*, from ventral side (after Ménézin). *a* Male; *HG* sucker; *b* young female in copulatory stage; *c* female ready to lay.

Pterophagus, *Heteropsorus*, *Epidermoptes*, *Rivoltasia*, *Pachylichus*, *Microlichus*, *Dermatium*.

Fam. 11. **Tyroglyphidae.** (Fig. 566.) Integument smooth and soft or with low protuberances, never parallel folds; the legs usually have a single claw, often with a leaf-like but not stalked sucker. They mostly have a wandering larval stage and with few exceptions, which are parasitic, live amongst carrion, cheese and other organic matter. *Histiostoma* and

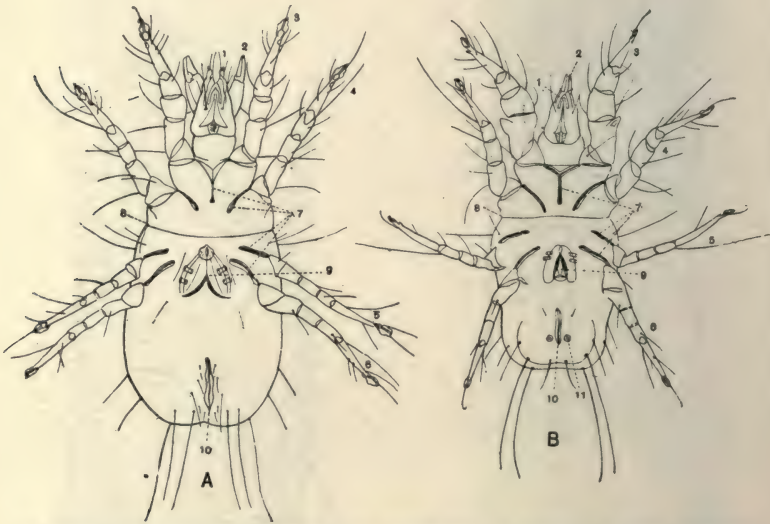


FIG. 566.—*Tyroglyphus siro*, seen from the ventral side. A female; B male. Magnified (from Leuckart and Nitsche). 1 Pedipalpi; 2 chelicerae; 3, 4, 5, 6 first, second, third and fourth walking legs; 7 chitinous thickenings supporting legs; 8 furrow round body; 9 reproductive opening, flanked by two suckers on each side; 10 anus; 11 suckers at side of anus.

Nodipalpus mostly on plants or manure; *Chortoglyphus*, *Lentungula* on algae; *Aleurobius* in meal; *Tyroglyphus*, the cheese mite; *Histiogaster* on plants and fungi; *Rhizoglyphus* and *Hericia* on the bark of trees and vines; *Glycyphagus* on dust, in mole holes and moss; *Saproglyphus* on fungi; *Carpoglyphus* on fruit and jams; *Trichotarsus* in insect nests; *Dermacarus* on *Sciurus*, *Pullea* on beetles.

Sub-order 6. VERMIFORMIA.

Degenerate acarines, with no tracheae and no eyes, the posterior end of the body is produced into an annulated tail. The four pairs of legs are short and 3-jointed.

Fam. 12. **Demodicidae.** Microscopic mites which live in the hair follicles and sweat glands of certain Mammals and cause the disease known as "follicular mange." The larva is legless or with very short legs. There are 5 well recognized species, and several doubtful ones. *Demodex folliculorum* (Fig. 567) lives on man and is often seen in follicles on the nose, it is

probably cosmopolitan. *D. canis* attacks dogs, *D. caprae* the European *Capra hircus*, *D. phylloides* the pig, and *D. bovis* the ox.

Sub-order 7. TETRAPODA.

Degenerate mites without tracheae, the body is elongate and the posterior part is ringed, the 3rd and 4th appendages are lengthened the 5th and 6th absent. They cause and inhabit plant-galls.

Fam. 13. **Eriophyidae** * (**Phytoptidae**). Fig. 555. The mites of this family form galls, with a single chamber opening to the exterior by a pore protected by hairs. The chamber, unlike those of insect-formed galls each of which contains one insect, contains a considerable number of mites which live on the vegetable hairs growing on the inner wall of the chamber. *Eriophyes*, with some 150 species on all sorts of plants; *E. tiliae* forms the well known "nail" galls on the Lime leaf and *E. ribis* is at present doing much harm to black currants in Great Britain; *Monochetus* with one species on the Beech; *Phyllocoptes* some 50 species on many plants; *Anthocoptes* many species on trees; *Tegonotus* 3 species on three natural orders of plants; *Epitrimerus* 14 species on nine different natural orders; *Oxypleurites* 6 species on 5 different natural orders; and *Paraphytoptus* one species on Artemisia.



FIG. 567.—*Demodex folliculorum* (after Ménézin), strongly magnified; *Kt*, pedipalpus.

APPENDIX I TO THE ARACHNIDA.

We have placed the Tardigrada and the Pentastomida in appendices to the group Arachnida because they show distinct Arthropod characters and their affinities point more closely to the Arachnida than to any other group of Arthropods.

Order TARDIGRADA.

Minute, cryptozoic animals with four pairs of stumpy clawed legs, suctorial mouth and oral armature, without circulatory and respiratory systems and connective tissue.

The Tardigrada are cryptozoic, living a retired life amongst moss and debris collected in gutters, of roofs, on tree-trunks †

* Nalepa, *Das Tierreich*, 4 Lieferung, Eriophyidae (Phytoptidae).

† Plate, *Zool. Jahrb. Anat.*, iii, 1889. v. Erlanger, 1895, *Morph. Jahrb.*, xxii, 1895. Richters, *Zool. Anz.*, xxxi, 1907, p. 197. and Heinis, *Zool. Anz.*, xxxii., 1908, p. 633.

or in ditches. They are very widely distributed and very common yet they are seldom seen. Their small size aids them to elude observation, they average but 0.3 mm. to 1 mm. in length.

The body of a Tardigrade is enclosed in a cuticle and this and the underlying tissues are often transparent, and, as many of the cells are large and symmetrically placed and above all there is no connective tissue to blur the organs, they form a very favourite object for the inspection of microscopists. The cuticle is usually of a uniform thickness all over the body, but in *Echiniscus* it is thickened into certain dorsal plates. The forked claws at the end of each of the eight legs are also cuticular. From time to time the cuticle is cast and it is not unusual to find a Tardigrade imprisoned in two cuticles the outer one of which

he has cast but not yet thrown off. *Macrobiotus* lays its egg in its cast cuticle.

The shape of a Tardigrade varies within limits but it is usually somewhat squat; many have roughly speaking about the proportions of a land tortoise and their movements are as deliberate as those of the Chelonians. Anteriorly is situated the mouth and posteriorly the anus. On each side are four legs, the anterior pair pointing forward, the two middle pairs forward or outward, the hindmost pair backward, and each leg terminates in two forked claws which assist the creature to crawl about (Fig 568). *Lydella* is described as having two joints to each leg, but with this exception the legs are unjointed.

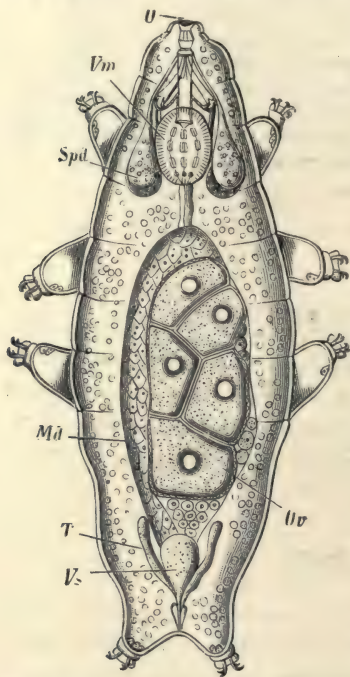


FIG. 568.—*Macrobiotus schultzei* (after Greeff). *O* mouth; *Vm* pharynx; *Md* stomach; *Spd* salivary glands; *Ov* ovary; *T* Malpizhian tubules; *Vs* accessory gland.

The epidermal cells which underlie the cuticle are arranged in very definite rows; they form but a single layer and the con-

spicuous nuclei are placed in each cell in a corresponding position to that of the corresponding cell of the other side of the body. At the end of the limbs and around the orifices into the body the cells are heaped up, but elsewhere the cuticle and the single-layered epidermis surround a spacious body-cavity. This cavity contains the viscera which are bathed by an uncoagulable fluid. Numerous corpuscles, increasing in number as the animal grows old, float in this fluid and these in well-nourished individuals are packed with food reserves. The body-cavity is traversed both by muscle-fibres and by nerves symmetrically placed, and the curious absence of connective tissue, associated in many cases with the great transparency of the tissues, allows these to be readily investigated. There are also ventral, dorsal, and lateral bands of muscles, and others that move the limbs and teeth.

The mouth commences with what is termed the oral cavity, which may or may not be surrounded by certain cuticular rings; this opens behind into a narrow tube lined by chitin, the mouth tube. The two chitinous teeth or stylets project into the mouth tube in certain species of *Macrobiotus* and *Doyeria* but into the oral cavity in *Echiniscus*, *Milnesium* and some species of *Macrobiotus*. These teeth or stylets may be strengthened by a calcareous deposit. They are moved by three muscles attached to their hinder ends. The mouth-tube passes into a stout muscular pharynx, circular in outline with radiating muscle-fibres. When these contract the lumen is enlarged and the fluid food—usually the cell-sap of some moss cell which has been pierced by the stylets—is drawn in. Two glands, called salivary, open into the mouth; in some species their secretion is considered poisonous. The pharynx is succeeded by an oesophagus which may be reduced to almost nothing; this opens into a capacious stomach whose walls consist of a layer of very definitely hexagonal cells. Posteriorly this passes into a rectum, which unites with the duct of the excretory organs and of the reproductive organs; the resulting cloaca opens by a transverse slit between the last pair of legs.

The excretory function is said to be carried out by a pair of lateral caeca which open into the rectum. These recall the somewhat similar diverticula of certain mites and probably represent malpighian tubules.

There are no special organs of circulation or of respiration. The corpusculated fluid in the body-cavity is moved about intermittently by the movements of the legs, teeth, etc., and this fluid and the tissues must be oxygenated through the thin cuticle.

The nervous system comprises a supraoesophageal ganglion, an infraoesophageal ganglion, and a ventral ladder of four ganglia. The supra-oesophageal ganglion is somewhat rounded; posteriorly it is produced on each side into two lobes, one of which bears an eye; close to this a slender nerve emerges which runs straight to the first ventral ganglion. The large mass of the brain is curved round the oral cavity and enters the sub-oesophageal ganglion. This is united to the first ventral ganglion, and this in its turn to the next, and so on, by widely divaricated longitudinal commissures. The transparency of the tissues and the absence of connective tissue allow the nerves supplying the curiously symmetrical muscles to be readily traced to their nerve-plate or nerve-end-plate.

There has been much confusion about the sex of the Tardigrada. For a long time they were thought to be hermaphrodite, but more recently the genus *Macrobiotus* has been shown to be bisexual, and probably the same holds good for all the genera. The males are smaller than the females and much rarer. The testes and ovary open into the intestine near the posterior end and each is provided with a dorsally placed accessory gland.

Only some of the eggs develop, and this they do at the expense of the others. The segmentation of the egg of *M. macronyx* is total and equal, and a typical blastula and gastrula are formed. The blastopore closes and the anus ultimately arises at the same spot. Four pair of mesoblastic somites are formed and give origin to the coelom and to the musculature. Both the malpighian tubules and the testes and ovary arise as diverticula of the alimentary canal.

The details of the development seem to be primitive in their nature, and afford no support to the view that the Tardigrada are in any way degenerate. They may be regarded as the simplest and lowest group of Arthropods, but they show little affinity to any of the now existing forms. The fact that different authorities have placed the Tardigrada near the Crustacea, the Rotifers, the Annelids, the Acarina, the Pentastomida, and

the Myzostomida shows that their position in the animal kingdom is very indeterminate.

Those Tardigrades which live amongst moss, like some Rotifers and Nematodes, possess remarkable powers of undergoing desiccation without being injured in any way by the process of drying up. As the moisture diminishes, the little creatures cease to move and begin to shrivel up until they resemble a small grain of sand. After rain or heavy dew, however, they slowly revive, swell up to their former size, and behave as if nothing had interfered with their former activity.

Fam. 1. **Echiniscidae** with the characters of the order.

The following genera are recognized:—*Echiniscus* C. Sch. (= *Eurydium* Doy.) a widely distributed genus found in the Arctic region and on mountains up to 11,000 feet and elsewhere. There are numerous species and one sub-genus *Echiniscoides* of which the single species *Echiniscoides sigismundi* lives amongst sea-weed. *Microlyda* (*Lydella*), one species with elongated legs, is another marine form. *Macrobiotus* with many species lives amongst moss or in fresh-water. *Doyeria* with a single species also lives amongst moss. *Diphascon* with several species occurs in Europe, Spitsbergen and Chili. *Milnesium* has two species.

APPENDIX II TO THE ARACHNIDA.*

Order PENTASTOMIDA.

Elongated, vermiform parasites with ringed bodies, a pair of claws on both sides of the mouth, no respiratory or circulatory organs, larval form present.

The Pentastomida, with but three genera, *Porocephalus*, *Lingua-tula* and *Reighardia*,† are exclusively parasitic and pass the adult stages of their life in the noses and adjacent sinuses of flesh-eating vertebrates. Their eggs when fertilized, are sneezed out or coughed up, and, falling on grass or plants, are eaten by some vegetable-feeding animal. When they reach the stomach,

* W. Stiles, *Zeitschr. wiss. Zool.*, lii, 1891. Lohrmann, *Arch. Naturg.*, lv, 1889. A. E. Shipley, *Arch. Parasit.*, i, 1898.

† H. B. Ward, *P. Amer. Ass.*, 1899, p. 254.

the egg-shell disappears and the issuing larva makes its way into the tissues surrounding the alimentary canal. Here it comes to rest and encysts, until this first host falls a prey to some carnivorous animal, when the parasite makes its way into the nose or lungs and becomes in a short time mature.

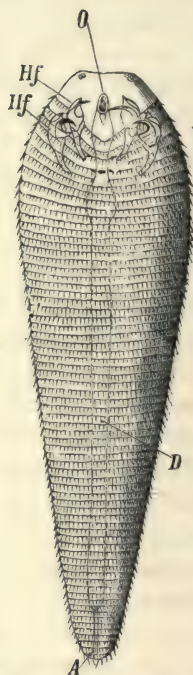


FIG. 569.—*Pentastomum teneioides*. O Mouth; Hf the hooks; D intestine; A anus.

Like most Entozoa and other animals that live in the dark, the members of the Pentastomida are white unless tinged with the blood of their host which they suck. The body is either cylindrical or in the genus *Linguatula* somewhat flattened and lanceolate; it is more or less sharply ringed, but the annuli do not correspond with any internal segmentation and there is very little trace of segmentation in the body at any time of the life-history.

The anterior end of the body is separated off from the rest sometimes by quite a narrow neck. This head bears the mouth and two pairs of chitinous hooks. It never shows any annulations. The hooks have expanded chitinous basal plates into which muscles are inserted. The hooks themselves are strongly re-

curved and can be protruded and retracted with ease.

Certain papillae are symmetrically scattered over the head, and others are arranged over the anterior half of each annulus. These correspond with epidermal pits. There is also a pair of large papillae, which lie in front of the inner pair of hooks and bear the openings of the hook-glands.

The body is ensheathed in a cuticle which is secreted by the epidermal cells. The epidermal glands are special aggregations of these cells with a short lumen opening on the papillae; these openings were formerly called stigmata. Some authorities regard them as having an excretory function.* The hook-glands however are much larger structures, and extend on each side of the

* Baldwin Spencer, *Q. J. Mic. Sci.*, xxxiv, 1893, p. 1.

alimentary canal to near the hinder end of the body. Anteriorly the right and left glands fuse to form the head-gland which fills up a good deal of the space within the head. From the head-gland three ducts arise on each side, one passes to each of the large papillae and one to the base of each hook; it has been suggested that the glands secrete an irritating fluid which stimulates the flow of blood and prevents a coagulum being formed.

Below the epidermis lies a layer of circular muscles and beneath them a longitudinal layer. As in *Polygordius*, *Peripatus* and other primitive animals, a sheet of muscle fibres runs from each side of the body towards the ventral median line thus dividing the body cavity into three chambers. Other muscles move the hooks, and there are several which by contracting enlarge the lumen of the pharynx which thus acts as a sucking-pump. The muscles are striated.

The mouth is borne on a prominence; it leads into a pharynx which passes backwards and upwards and soon opens into an oesophagus. This passes upwards and projects into the lumen of the stomach, thus forming a valve which prevents the regurgitation of the fluid food. The stomach or mid-gut is large and stretches back to near the hind end of the body; here it narrows and passes into a short rectum which opens by a terminal anus. The pharynx and oesophagus and the rectum are lined with chitin and represent the stomodaeum and protodaeum respectively.

The nervous system consists of a large ventral ganglion which gives off two cords devoid of ganglionic cells which meet and fuse above the oesophagus. From each side eight nerves arise which supply the neighbouring structures, and behind, a ninth pair, the largest of all, runs backward along the ventral surface of the animal to the posterior end. The only sense organs are certain paired sense papillae situated on the head. There are no specialized respiratory or circulatory organs and no organs comparable with nephridia, coxal glands or malpighian tubules.

The sexes are separated in the Pentastomida. The males are smaller than the females and are said to be the more numerous. The testis is a cylindrical sac closed behind, lying dorsally above the stomach. Anteriorly the sac splits and passes into two lateral ducts, the vesiculae seminales, which encircle the alimentary canal and pierce through the tissue of the hook-glands. The

vesiculae pass into a chitin-lined vas deferens which receives the contents of large backwardly directed ejaculatory glands, one on each side. The vasa deferentia then traverse a cirrus bulb which receives on one side a cirrus-sac and on the other a dilator-rod-sac, both of which assist in copulation. The two ducts then unite and open by a median ventral pore a little posterior to the mouth.

The ovary is also a median dorsal sac, which splits anteriorly into a right and left oviduct, which pierce the hook-gland and encircle the stomach and the ninth pair of nerves. The oviducts unite ventrally and at their point of union receive the ducts of two receptacula seminis or spermathecae which as a rule contain numerous spermatozoa. The uterus formed by the united oviducts is continued along the ventral surface of the body as a coiled tube often crowded with fertilized eggs; as many as half a million may be found. The uterus opens by a narrow vagina in the median ventral line a little in front of the anus.

The ova undergo a considerable part of their development within the body of the mother. In those forms which live in the nasal passages, the eggs when laid leave the host with its nasal excretions; but in those which inhabit the lungs, the eggs pass down the alimentary canal and leave the host's body with the faeces. For their further development it is necessary that they be eaten by some other animal, and this second or larval host is as a rule herbivorous. The larva, which emerges when the egg-shell is dissolved in the stomach of the second host, is globular with a tail and two pairs of appendages ending in hooks. Anteriorly is a boring apparatus of chitinous rods. By means of this armature the larva bores through the stomach walls and comes to rest in some organ, often the liver. Here a cyst is formed in which it lies. It moults a few times and loses its limbs, but its internal organs are maturing and the annulations appear, arising first about the middle of the body. After a quiescent period of some months the larva again becomes active and wanders through the tissues of its second host, a proceeding which is sometimes fatal to the latter. If the second host should now be eaten by a member of the first, i.e. some carnivorous creature, the larva makes its way into the nasal passages or lungs as the case may be, and after a final moult becomes adult.

The larval form with its two pairs of clawed limbs recalls the

Tardigrades and certain aberrant Acarines such as *Phytoptus*, and the arrangement of the reproductive organs is like that of many Arthropods. The other features of their anatomy and

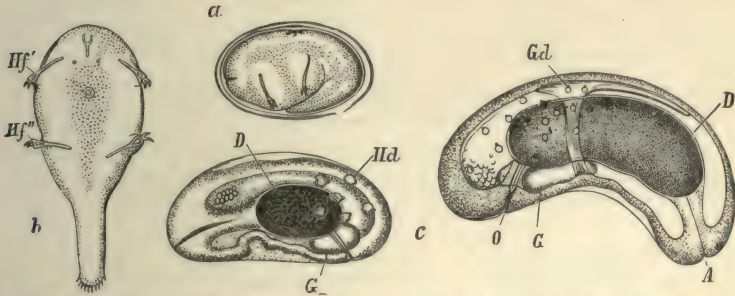


FIG. 570.—Young forms of *Pentastomum taenioides* (after R. Leuckart). *a* Egg with embryo; *b* embryo with two pairs of hooked feet, *Hf'* and *Hf''*; *c* larva from liver of rabbit; *G* ganglion; *D* intestine; *Hd* skin glands; *d* older larva; *O* mouth; *A* anus; *Gd* genital glands.

of their life-history is however so peculiar that it seems wiser to regard them as an appendix to, rather than an Order of, the Arachnida.

Fam 1. **Linguatulidae** with the characters of the order.

There are three genera. 1. *Linguatula* Frohlich with a flattened, turbellarian-shaped body, the body cavity extending into the lateral wings which are crenelated at the edge. Species have been found in a fresh-water South American fish *Acara* and are probably larvae, in the nose and trachea of *Felis onca*, in the throat of a Caiman, and the commonest of all *L. taenioides* in the nasal passages of dog and wolf, the fox, horse, sheep, mule and man; the larva of the latter has been found in the rabbit, hare, guinea pig, ox, pig, horse and a few other animals. 2. *Porocephalus* Humboldt (*Pentastoma* Rud). The body is cylindrical with a more or less well developed head. This genus usually inhabits the lungs. It occurs in large snakes, crocodiles, lizards, some birds, e.g. sea-gulls, tortoises and many members of the order Carnivora. 3. *Reighardia*, devoid of annulations, transparent, with poorly developed hooks but a mouth armature, is found in the air sacs of Bonaparte's Gull and in the common tern of North America.

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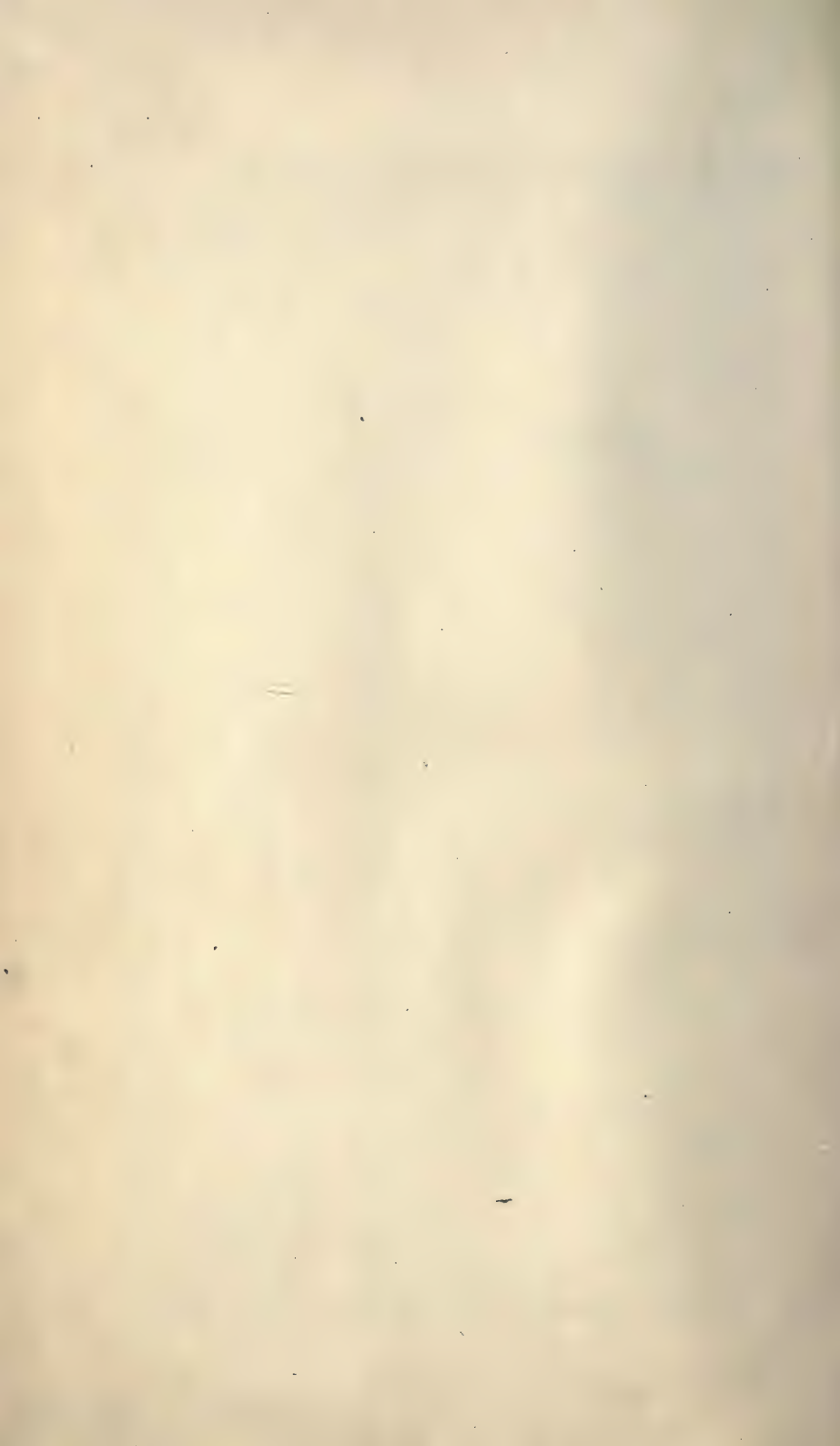
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